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COMPARATIVE FUNCTIONAL ANATOMY OF THE NANDIDAE (PISCES: TELEOSTEI)

KAREL F. LIEM

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COMPARATIVE FUNCTIONAL ANATOMY OF THE NANDIDAE (PISCES: TELEOSTEI)

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Introduction

It is generally accepted that the percoid fish family Nandidae exhibits the most disrupted geographical distribution known in freshwater teleosts of the primary division. *Nandus* is known from India and the Indomalaysian Archipelago; *Afronandus* and *Polycentropsis* from West Africa; and *Polycentrus* and *Monocirrhus* from South America. Although implications have been made that nandids represent a uniform assemblage of closely related genera (Myers, 1938), fossil representatives are unknown and there are no clues regarding dispersal routes.

The phylogenetic relationships between the nandid genera and the evolutionary status of the Nandidae in the order Percoidei are still a matter of speculation.

Regan (1913) distinguished two separate families, the Nandidae (including *Nandus, Polycentrus, Monocirrhus,* and *Polycentropsis*) and the Pristolepidae (including *Badis* and *Pristolepis*).

Jordan (1923) also recognized two families. However, his grouping differed significantly from that of Regan: The paleotropical Nandidae included *Badis, Pristolepis,* and *Nandus* and the Polycentridae with the neotropical genera *Polycentrus* and *Monocirrhus,* and the African genus *Polycentropsis.*

Smith and Bailey (1962) recognized only one family, Nandidae, which includes *Pristolepis.*

Freihofer (1963) using neurological evidence recognized two families: Nandidae (with *Badis, Nandus, Polycentrus, Polycentropsis,* and *Monocirrhus*) and Pristolepidae (with *Pristolepis*).

Gosline (1966) has pointed out the significant differences between the Pristolepidae and Nandidae in respect to the presence or absence of a scaly axillary process and the feeding apparatus.

Barlow *et al.* (1968) studied the ethology, osteology, and larvae of *Badis.* They proposed a new monotypic family Badidae that may be related to the Anabantoidei. Certainly, *Badis* differs significantly from the Nandidae and *Pristolepis.*

The delineation and definition of the family Nandidae remain at best unclear. Regan (1913) studied the osteology only in general terms. Khandelwal and Mittal (1965) have described the skull of one species, *Nandus nandus,* with no attempt to compare it with other nandids. Monod (1968) studied the caudal skeleton of two genera. The lack of adequate morphological data on a comparative basis does not eliminate the possibility of unrecognized convergence in the Asiatic, African, and South American forms. Parallel morphology in these geographically separated genera may be correlated with identical predatory feeding mechanisms leaving the boundaries of the family obscure. It is therefore not surprising that much disagreement exists among recent ichthyologists concerning the taxonomic status of the nandid genera and the boundaries of the family.

The original purpose of this study was to define the family Nandidae on a broad morphological basis. Comparative osteological data were collected and analyzed from *Nandus, Afronandus, Polycentropsis, Polycentrus, Monocirrhus, Badis, Pristolepis,* and from the allegedly related *Datnioides* and *Lobotes.* It was hoped that osteology would give us sufficient clues to the phylogenetic relationships between the nandid genera and the relationships of the family as a whole to other percoids.

However, in the succeeding stages of this study more emphasis was laid on feeding mechanisms. Functional analysis of the feeding apparatus may separate the convergent features from those that reflect phylogenetic affinities. The arthrology, ligamentous system, and myology of the jaw apparatus and branchial basket became the focus of attention. The various movements of the different components were analyzed by direct observations and motion pictures of live fishes in the aquarium. A thorough functional analysis of this group may lead to an understanding of the basic adaptive factors underlying the specialized predatory feeding mechanisms of the nandids. The nandids are well known for their extraordinary predatory habits, devouring prey up to three-quarters of their own body-length, and consuming their own body-weight in food daily. The nandids exhibit extreme morphological specializations correlated with exceptionally well-developed predatory habits. The adaptive significance of the specialized structures and functional units may give us clues to the causal evolutionary factors underlying the specialized nandid morphology.

Material and Methods

The descriptive part of this study is based on the specimens listed in Table 1. Most specimens have been cleared with the enzyme method (purified trypsin powder) and stained with sodium alizarin sulfonate following Taylor (1967). The muscles were studied from specimens fixed in either formalin, alcohol, or standard embalming solution. Some of the joints have been studied from serial sections of paraffin-embedded material, stained with Harris Hematoxylin and Eosin Y, and Mallory's modified triple stain. The drawings were made with the camera lucida of the Wild-M5 stereoscopic dissecting microscope.

To enhance the clarity of this account, the specific techniques used in motion analysis have been included in the appropriate sections of the text.

Osteology

The skull is divided into functional units as proposed by Liem (1967a, b). The following units are recognized and discussed on a comparative basis: neurocranium and sensory capsules, suspensory apparatus, jaw apparatus, opercular apparatus, hyoid apparatus, pectoral girdle, and branchial apparatus.

NEUROCRANIUM AND SENSORY CAPSULES

In dorsal and ventral views the nandid neurocranium is more or less rectangular. The dorsal surface is flat or somewhat convex. The cranial base exhibits an angle at the level of the posterior border of the orbit in a lateral view, except in *Nandus* and *Afronandus* in which the base is straight. The angle of the cranial base is most acute in *Polycentropsis*. The post-temporal fossae are moderately developed.

All nandids possess a very prominent median depression, the *rostral fossa,* housing the ascending processes of the premaxillae. The ethmoid and frontals contribute to the floor of the rostral fossa. In *Monocirrhus* the supraoccipital forms part of the posterior floor of the rostral fossa. *Nandus* and *Afronandus* possess fontanelles in the floor of the rostral fossa in the anteromedial corners of the frontals. The least extensive rostral fossa, reaching posteriorly to the level of the posterior border of the orbit, is found in *Afronandus*. In all other nandids the rostral fossa reaches posteriorly to the supraoccipital and in *Monocirrhus* the fossa extends over the anterior tip of the supraoccipital.

Three crests are discernible on the dorsal surface of the nandid neurocranium. The paired parietal crests are the least developed in *Afronandus,* in which each crest is restricted to the epiotic and the posterior half of the parietal. In all other nandids the crest is higher and extends over the posterior half of the frontals, the entire parietal and epiotic. The median supraoccipital crest is restricted to the posterior one-fourth of the supraoccipital in *Monocirrhus*. The other nandids possess a supraoccipital crest that runs throughout the length of the supraoccipital. Anteriorly, the supraoccipital crest splits to

Table 1.—List of Specimens Studied

Taxa	Museum[1] number	Locality	Number of specimens
Nandidae			
Nandus nebulosus	FMNH 68448	N. Borneo	4
Nandus nebulosus	RNHL 78779	Java	1
Nandus nandus	BM 35.350	Calcutta	1
Afronandus sheljuzkhoi	FMNH 74584	Ghana	1
Afronandus sheljuzkhoi	BM 35.355	Abidjan	2
Polycentropsis abbreviata	NHK	Niger Delta	3
Polycentropsis abbreviata	BM 35.380	Niger Delta	1
Polycentrus schomburgkii	FMNH 76007	S. America	5
Monocirrhus polyacanthus	FMNH 76004	S. America	7
Badidae			
Badis badis	FMNH 76044		5
Pristolepidae			
Pristolepis fasciatus	FMNH 60268	Malay Peninsula	3
Pristolepis fasciatus	BM 35.230	Sittang River	1
Pristolepis fasciatus	RNHL	Sumatra	1
Lobotidae			
Lobotes auctorus	RNHL		1
Lobotes auctorus	BM 31.900		1
Datnioides polota	RNHL		1
Datnioides polota	RNHL 18	Borneo	1
Datnioides polota	RNHL 8129	Malay Peninsula	1
Gerridae			
Gerres rhombeus	BM 32.020		1
Lutjanidae			
Lutjanus marginatus	BM 31.540		1
Lethrinidae			
Lethrinus striatus	BM 33.020		1
Lethrinus nebulosus	BM 33.020	Aden	1

[1] BM, British Museum; FMNH, Field Museum of Natural History; NHK, Naturhistoriske Museum Kopenhagen; RNHL, Rijksmuseum van Natuurlijke Historie, Leiden.

continue along each lateral rim of the rostral fossa except in *Monocirrhus,* which lacks the anterior extensions of the crest.

Nasal region.—The *nasals* (Figs. 1–8: N) are well developed except in *Afronandus.* They are elongate bones bordering the lateral walls of the anterior portion of the rostral fossa. Each nasal articulates with the frontal posteriorly and the prefrontal-lateral ethmoid posterolaterally. In *Nandus* the nasals are somewhat expanded, while in the other genera they are rodlike, with concave lateral borders and convex medial borders. The most elongate nasals are found in *Monocirrhus* and *Polycentropsis.*

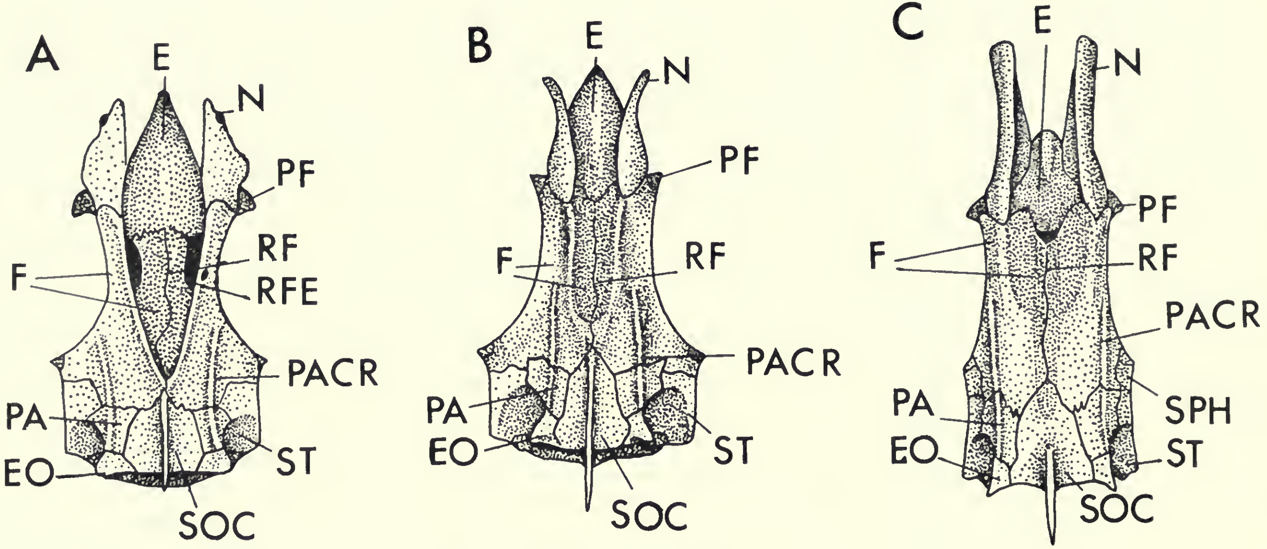

FIG. 1. Dorsal aspect of neurocranium of: A, *Nandus nebulosus*. B, *Polycentrus schomburgkii*. C, *Monocirrhus polyacanthus*. E, ethmoid; EO, epiotic; F, frontal; N, nasal; PA, parietal; PACR, parietal crest; PF, prefrontal-lateral ethmoid complex; RF, rostral fossa; RFE, rostral fontanelle; SOC, supraoccipital; SPH, sphenotic; ST, pterotic.

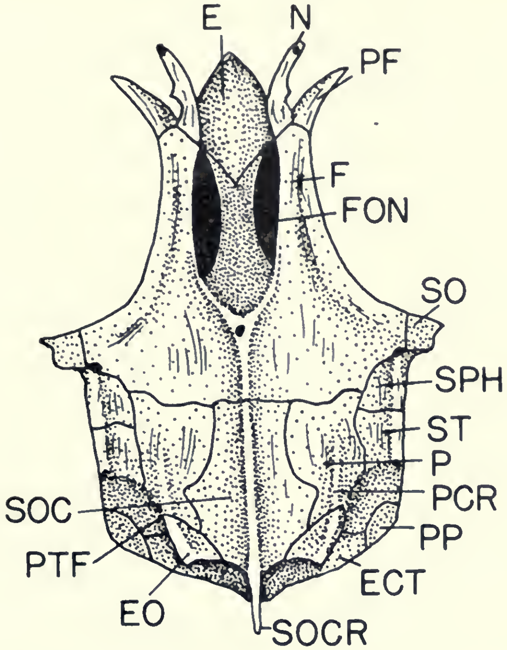

FIG. 2. Dorsal aspect of neurocranium of *Afronandus sheljuzkhoi.* E, ethmoid; ECT, exoccipital; EO, epiotic; F, frontal; FON, rostral fontanelle; N, nasal; P, parietal; PCR, parietal crest; PF, prefrontal-lateral ethmoid complex; PP, intercalary; PTF, post-temporal fossa; SO, circumorbital; SOC, supraoccipital; SOCR, supraoccipital crest; SPH, sphenotic; ST, pterotic.

The *prefrontal* and *lateral ethmoids* (Figs. 1–8: PF, LE) are fused into one complex bone forming the anterior border of the orbits. Dorsally, it contacts the posterolateral corner of the nasal and the anterolateral corner of the frontal. Medially, it approaches or contacts with the prevomer. In *Polycentropsis* a prominent ascending process of the prevomer is suturally united to the prefrontal-lateral ethmoid complex. A well-developed olfactory foramen is present in the center of the bone in frontal view. The lateral wing of the prefrontal-lateral ethmoid is not differentiated into an articular facet and serves as the attachment of the palato-prefrontal ligament. However, *Nandus* exhibits an exceptional condition in having two distinct articular facets on the prefrontal-lateral ethmoid complexes opposing corresponding articular facets on the palatine (Fig. 4).

The *ethmoid* (Figs. 1–8: E) is a prominent median bone forming the anterior half of the floor of the rostral fossa. The ethmoid is united to the frontals posteriorly, and with the prefrontal-lateral

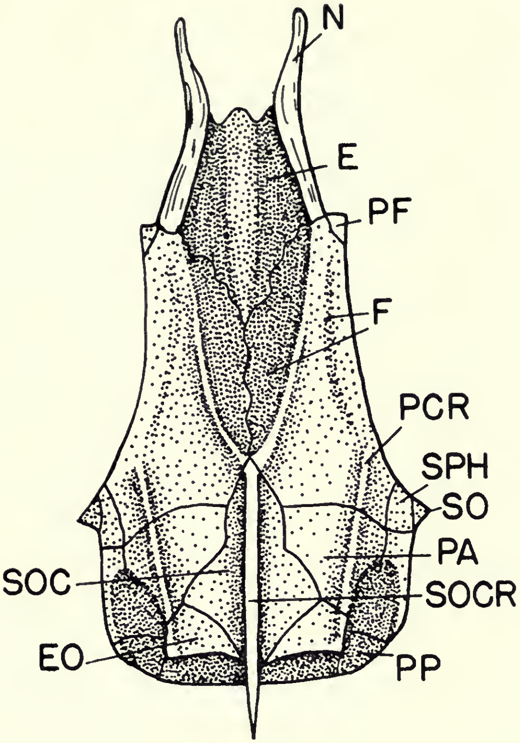

Fig. 3. Dorsal aspect of neurocranium of *Polycentropsis abbreviata*. E, ethmoid; EO, epiotic; F, frontal; N, nasal; PA, parietal; PCR, parietal crest; PF, prefrontal; PP, intercalary; SO, circumorbital; SOC, supraoccipital; SOCR, supraoccipital crest; SPH, sphenotic.

ethmoid complexes posterolaterally. The convex dorsal surface is elevated into a rather distinct blunt ridge in the median line. No contact is found between the ethmoid and prevomer.

The *prevomer* (Figs. 4–10: PV) is a relatively large bone forming the anterior third of the cranial base. The anterior portion is distinctly expanded. Anteroventrally, the bone is differentiated into a ventrally-directed, blunt crest serving as the site of attachment of the palatoprevomerine ligament. Posterodorsally, the prevomer expands to reach the ethmoid and prefrontal-lateral ethmoid. In *Polycentropsis* a distinct ascending process is differentiated to join suturally with an anteroventrally-directed process of the prefrontal-lateral ethmoid. Posteriorly, the prevomer tapers into a slender rod entering the anterior shaft of the parasphenoid. The prevomer is toothless, except in *Nandus* (Fig. 4).

Orbital region.—The *frontals* (Figs. 1, 6, 8, 10: F) are large bones
rming the anterior two-thirds of the cerebral skull. Each frontal
bordered by the nasal, prefrontal-lateral ethmoid and ethmoid an-
riorly; the sphenotic and circumorbital laterally; and the supra-
mporal, parietal, and supraoccipital posteriorly. The frontals are
ined to each other by an undulating suture. Anteromedially, they
ntribute to the floor of the rostral fossa. In *Nandus* and *Afronan-
us* large rostral fontanelles (Figs. 1, 2: RFE, FON) are present in
e portion of the frontal contributing to the rostral fossa. A well-
eveloped longitudinal parietal crest runs parallel to the lateral bor-
er of the cerebral skull, originating from the parietal suture. *Afro-
ndus* lacks the parietal crest on the frontal (Fig. 2).

The *pterosphenoids* (pleurosphenoids) are small, rectangular bones
rming the dorsal corners of the posteromedial wall of the orbits
'igs. 6, 8, 9: PLS). In *Polycentrus* and *Monocirrhus* the ptero-
henoids are joined anteriorly with the orbital lamina of the frontal.
ı *Nandus, Afronandus,* and *Polycentropsis* the pterosphenoid is in
more transverse position in the orbit and is widely separated from
e posterior border of the orbital lamina of the frontal. Posteriorly,
e pterosphenoid is joined to the prootic.

The *basisphenoid* is V-shaped in frontal view and forms the floor
the orbital opening of the brain case. The ventral part of the
asisphenoid reaches the parasphenoid. It divides the opening of
e myodome (Figs. 4–9: BS, BAS).

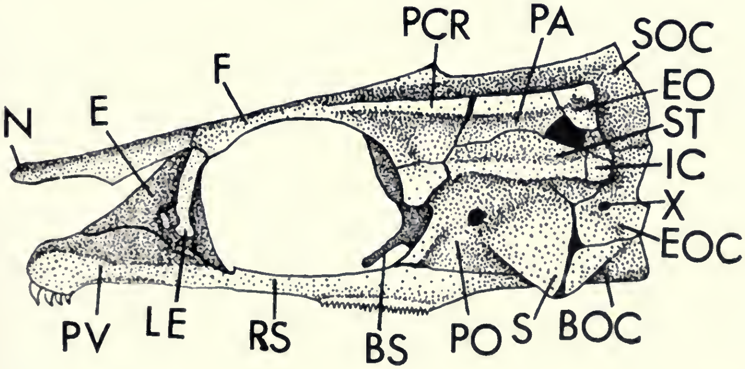

FIG. 4. Lateral view of neurocranium of *Nandus nebulosus*. BOC, basioccip-
al; BS, basisphenoid; E, ethmoid; EO, epiotic; EOC, exoccipital; F, frontal;
, intercalary; LE, lateral ethmoid with articular surfaces; N, nasal; PA, parietal;
CR, parietal crest; PO, prootic; PV, prevomer; RS, parasphenoid; S, saccular
ılla; SOC, supraoccipital; ST, pterotic; X, foramen for vagus.

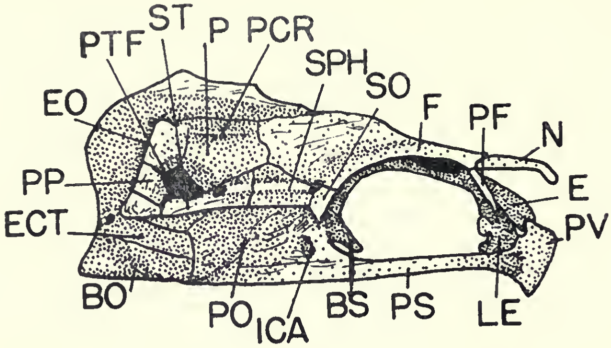

FIG. 5. Lateral view of neurocranium of *Afronandus sheljuzkoi*. BO, basioccipital; BS, basisphenoid; E, ethmoid; ECT, exoccipital; EO, epiotic; F, frontal; ICA, foramen for internal carotid artery; LE, lateral ethmoid; N, nasal; P, parietal; PCR, parietal crest; PF, prefrontal; PO, prootic; PP, intercalary; PS, parasphenoid; PTF, post-temporal fossa; PV, prevomer; SO, circumorbital; SPH, sphenotic; ST, pterotic.

The *circumorbitals* do not form a subocular shelf. The ventral margins of all circumorbitals are serrated in *Nandus* (Fig. 17: SO). In all other nandid genera the circumorbitals are non-serrate (Figs. 19–21: SO). In *Polycentropsis* the circumorbitals are interrupted, because the most anterior one is not ossified (Fig. 20).

The *lachrymal* is attached to the prefrontal-lateral ethmoid complex posterodorsally and articulated with the dorsal portion of the maxillary. Posteriorly, the bone is joined to the first circumorbital, except in *Polycentropsis*. The margins of the lachrymal are smooth in *Nandus, Afronandus,* and *Monocirrhus*. The ventral margin of the lachrymal is serrated in *Polycentropsis* and *Polycentrus* (Figs. 17–21: L). Anteriorly, the lachrymal tapers off in a slender projection. In *Afronandus* the lachrymal is small and triangular, with a very slender ventral projection.

Otic region.—The *sphenotic* is a small bone that is joined to the pterotic posteriorly and to the frontal anteriorly and medially (Figs. 1–3, 5, 10: SPH). No connections with the parietal are found. Ventrally, the sphenotic possesses a circular socket that receives the ball-like anterior head of the hyomandibular. The joint between the sphenotic fossa and the anterior head of the hyomandibular is synovial and allows a lateromedial motion of the latter. Laterally, the sphenotic is partially overlapped by the posterodorsal circumorbital. The sphenotic forms part of the posterior orbital wall.

Each *parietal* is bordered by the epiotic posteriorly; the pterotic laterally; the frontal anteriorly; and the supraoccipital medially

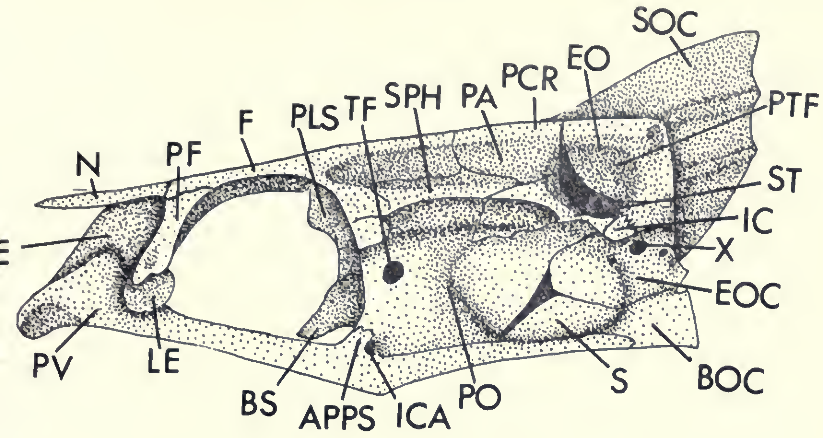

FIG. 6. Lateral view of neurocranium of *Polycentrus schomburgkii*. APPS, scending process of parasphenoid; BOC, basioccipital; BS, basisphenoid; E, ethnoid; EO, epiotic; EOC, exoccipital; F, frontal; IC, intercalary; ICA, foramen or internal carotid artery; LE, lateral ethmoid; N, nasal; PA, parietal; PCR, parietal crest; PF, prefrontal; PLS, pleurosphenoid; PO, prootic; PTF, post-temporal ossa; PV, prevomer; S, saccular bulla; SOC, supraoccipital; SPH, sphenotic; T, pterotic; TF, trigeminofacial chamber; X, foramen for vagus nerve.

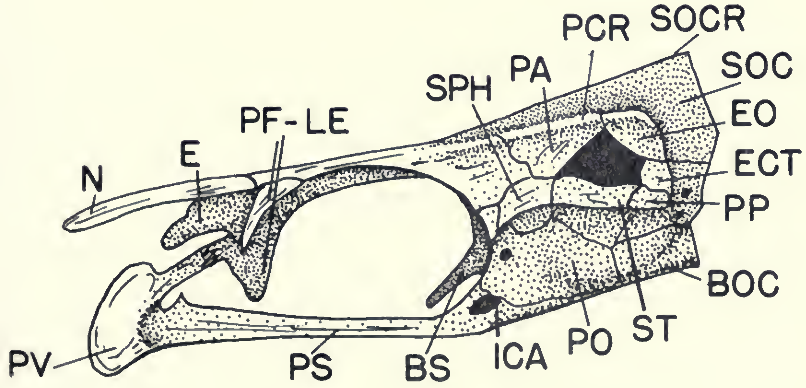

FIG. 7. Lateral view of neurocranium of *Polycentropsis abbreviata*. BOC, basiccipital; BS, basisphenoid; E, ethmoid; ECT, exoccipital; EO, epiotic; ICA, oramen for caratid; N, nasal; PA, parietal; PCR, parietal crest; PF-LE, prefrontalateral ethmoid complex; PO, prootic; PP, intercalary; PS, parasphenoid; PV, preomer; SOC, supraoccipital crest; SPH, sphenotic; ST, pterotic.

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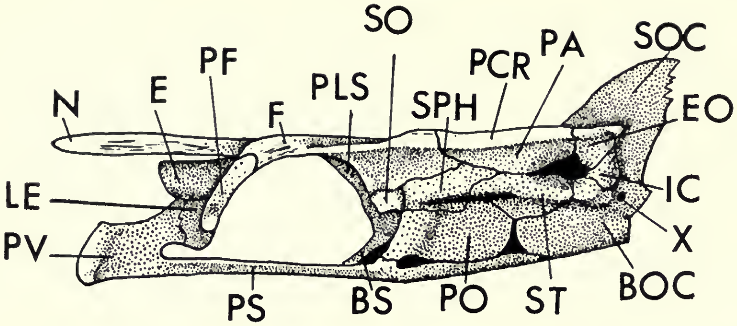

FIG. 8. Lateral view of neurocranium of *Monocirrhus polyacanthus*. BOC, basioccipital; BS, basisphenoid; E, ethmoid; EO, epiotic; F, frontal; IC, intercalary; LE, lateral ethmoid; N, nasal; PA, parietal; PCR, parietal crest; PF, prefrontal; PLS, pleurosphenoid; PO, prootic; PS, parasphenoid; PV, prevomer; SO, circumorbital; SOC, supraoccipital; SPH, sphenotic; ST, pterotic; X, foramen for vagus nerve.

(Figs. 1–4: PA, P). A conspicuous parietal crest runs along the entire length (in *Afronandus* restricted to the posterior half) of the bone, joining similar crests on the frontal and epiotic. The parietals of *Afronandus* are relatively larger than those in other nandids. The posterolateral border of the parietal forms part of the anteromedial wall of the post-temporal fossa.

The *extrascapulars* are absent.

The *pterotics* (supratemporal-intertemporal bones) form the major part of the wall and floor of the post-temporal fossa and the major portion of the hyomandibular facet (Figs. 1, 2, 4, 10: ST). Anteriorly, the pterotic is joined to the sphenotic, laterally to the frontal, parietal and epiotic. A distinct dilatator fossa is lacking. The main cephalic sensory canal from the supratemporal enters the bone through one pore on its posterodorsal edge and divides immediately, sending the preopercular canal ventrally through a foramen on the dorsolateral face of the preopercular, while the main branch passes forward through the pterotic to the sphenotic where it emerges into a pore. Ventrally, the pterotic is bordered by the prootic and exoccipital. The hyomandibular facet accommodates the posterior elongate head of the hyomandibular.

The *prootics* are the largest bones of the otic region. Each is joined to the parasphenoid ventrally, the basioccipital and exoccipital posteriorly, and the pterosphenoid and pterotic dorsolaterally (Figs. 4–10: PO). The ventral division of each prootic is made up of the

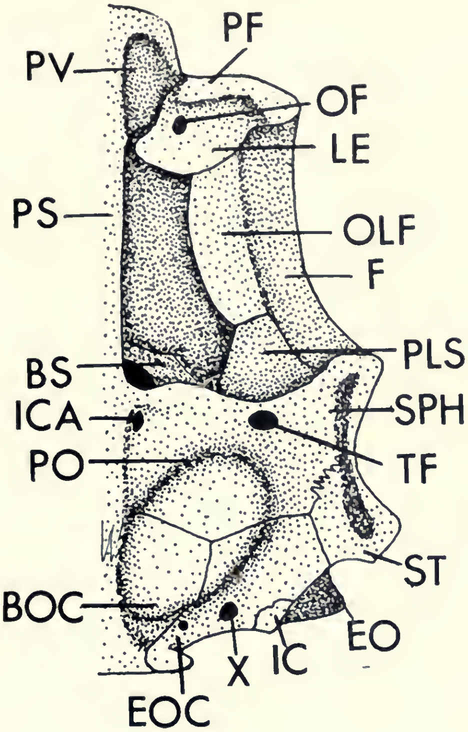

FIG. 9. Ventral view of left half of neurocranium of *Polycentrus schomburgkii*. BOC, basioccipital; BS, basisphenoid; EO, epiotic; EOC, exoccipital; F, frontal; IC, intercalary; ICA, foramen for internal carotid artery; LE, lateral ethmoid; OF, olfactory foramen; OLF, orbital lamella of frontal; PF, prefrontal; PLS, pleurosphenoid; PO, prootic; PS, parasphenoid; PV, prevomer; SPH, sphenotic; ST, pterotic; TF, trigeminofacial chamber; X, foramen for vagus nerve.

vertical bony laminae. The inner lamina joins the basioccipital posteriorly and separates the myodome from the otolith chamber, while the lateral lamina forms the outer wall of the skull and otolith chamber. Dorsally, the inner lamina curves medially, meeting its fellow from the opposite side, to form the prootic bridge that separates the cranial cavity from the myodome. The prootic does not contribute to the hyomandibular facet. The prootic contains the trigeminofacialis chamber. As in most advanced teleosts, this chamber is divided by a bony septum into a medial pars ganglionaris and a lateral pars jugularis. The pars ganglionaris is a recess on the internal face of the prootic. The pars jugularis has two external openings, an anterior one in the orbital face and a smaller posterior one on the lateral surface of the prootic. The posterior opening accommodates the

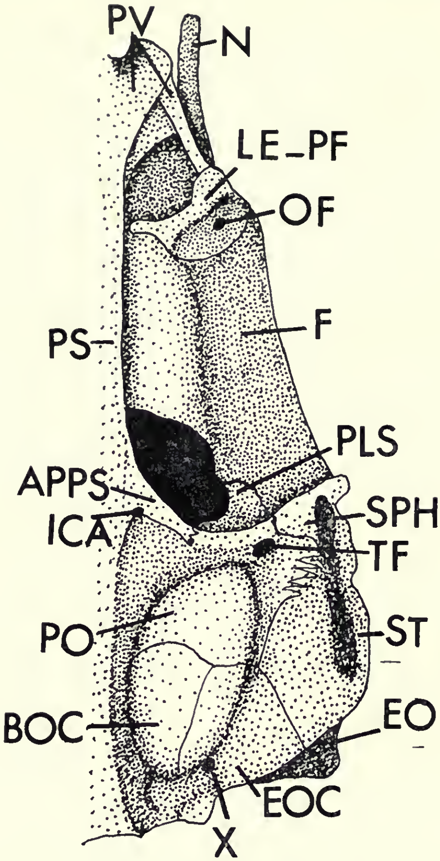

FIG. 10. Ventral view of left half of neurocranium of *Polycentropsis abbreviata*. APPS, ascending process of parasphenoid; BOC, basioccipital; EO, epiotic; EOC, exoccipital; F, frontal; ICA, foramen for internal carotid artery; LE-PF, lateral ethmoid-prefrontal complex; N, nasal; OF, olfactory foramen; PLS, pleurosphenoid; PO, prootic; PS, parasphenoid; PV, prevomer; SPH, sphenotic; ST, pterotic; TF, trigeminofacial chamber; X, foramen for vagus nerve.

hyomandibular trunk of the facial nerve, the jugular vein, and orbital artery. The anterior opening of the pars jugularis in the orbital face of the prootic transmits the trigeminal nerve and buccal branch of the facial nerve, the profundus branch of the trigeminal nerve, the superficial ophthalmic branches of the facial nerve, the otic branch of the facial nerve, the jugular vein, and orbital artery.

The *epiotics* form the posterior parts of the medial walls of the post-temporal fossae (Figs. 1-11: EO). The posterolateral corner of the dorsal surface is differentiated into a small facet to form a joint with the dorsal limb of the post-temporal. Internally, the epiotic gives rise to a distinct bony strut running anteroventrally to meet a similar strut from the prootic. Anteriorly, the epiotic is bordered by the parietal; medially, by the supraoccipital; and ventrally, by the pterotic and exoccipital.

Each *intercalary* is wedged in between the exoccipital and pterotic (Figs. 2–9, 11: PP, IC). The intercalaries are superficial dermal bones that do not contribute to the cranial vault. The intercalary forms part of the floor of the post-temporal fossa. The dorsal surface possesses a slightly elevated articular facet for articulation with the ventral fork of the post-temporal.

The *post-temporal* consists of a relatively small, elongate body with its long axis in a horizontal disposition (Fig. 26: PT). A pointed dorsal process projects from the anterodorsal corner in an anteromedial direction to articulate with the dorsal surface of the epiotic. Its anteroventral corner gives rise to a ventrally-directed ventral fork that articulates with the dorsal surface of the intercalary. The supracleithrum articulates with the ventromedial face of the post-temporal just posterior to the origin of the ventral fork.

The *supraoccipital* is a relatively large bone forming the posteromedian portion of the cranial roof. Anteriorly, the bone is joined with the frontals; laterally, with the frontal, parietal, and epiotic; and ventrally, with the exoccipital. In *Monocirrhus* the supraoccipital contributes to the rostral fossa, but this is not the case in any of the other nandid genera (Fig. 1: SOC). The supraoccipital crest is well developed in all genera running throughout the length of the bone (Figs. 2, 3: SOC), except in *Monocirrhus* in which it is confined to the posterior half. The occipital protuberance is well developed and contributes to the roof of the foramen magnum in all nandids (Fig. 11: SOC).

Each *exoccipital* meets ventrally with the basioccipital; anteriorly, with the pterotic and intercalary. Posteriorly, each exoccipital is differentiated into a well-developed condyle, which is elongate in the transverse axis. The exoccipitals do not meet above the foramen magnum (Fig. 11: EOC). Posterodorsally and toward the median line the exoccipitals articulate with the epiotics and supraoccipital. The exoccipital forms the posteromedial edge of the post-temporal fossa (Figs. 4–11: EOC, ECT). Lateral to the foramen magnum are a variable number (1–4) of small foramina for the occipital nerves. Anteroventrally, the exoccipital contributes to the posterodorsal corner of the otolith chamber. The lateral wall of the exoccipital possesses a small foramen that transmits the glossopharyngeal nerve and a larger vagus foramen.

Basicranial region.—The *basioccipital* forms the posteroventral part of the neurocranium (Figs. 4–11: BO, BOC). Anteriorly, it is joined with the parasphenoid and prootic, and dorsally with the exoccipital. Posteriorly, the basioccipital forms an occipital condyle with the notochord pit located off center toward the foramen magnum (Fig. 11). The anterodorsal wings of the basioccipital form the walls of the posterior parts of the saccular bulla.

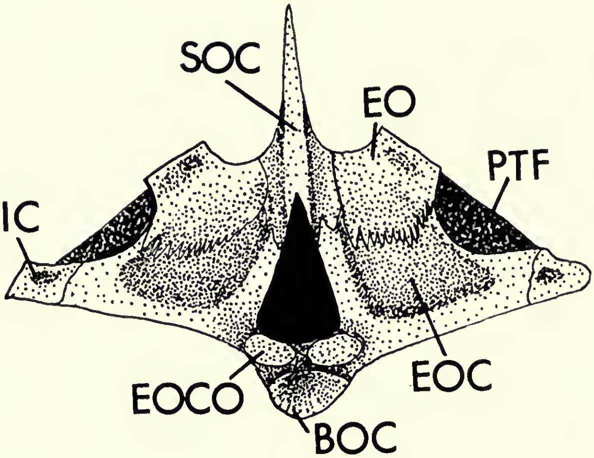

FIG. 11. Posterior view of neurocranium of *Polycentrus schomburgkii*. BOC, basioccipital; EO, epiotic; EOC, exoccipital; EOCO, exoccipital condyle; IC, intercalary; PTF, post-temporal fossa; SOC, supraoccipital.

The *parasphenoid* forms the greater part of the cranial basis (Fig. 4: RS, Figs. 5, 7–10: PS). The bone has a convex ventral border and is bent through an angle of approximately 30° at the level of the ascending process in *Polycentrus, Monocirrhus,* and *Polycentropsis*. The parasphenoid is nearly straight in *Nandus* and *Afronandus*. In *Nandus* a patch of villiform teeth is present (Fig. 4). The patch extends from a level corresponding to the most anterior extension of the parietal crest to a level just posterior to the foramen for the internal carotid artery. Parasphenoid teeth are wanting in the other genera. The ascending processes of the parasphenoid originate at the level of the basisphenoid pedicel. In the angle between the prootic and the posterior edge of the ascending process lies the foramen for the internal carotid artery. Anteriorly, the parasphenoid has a deep fossa to house

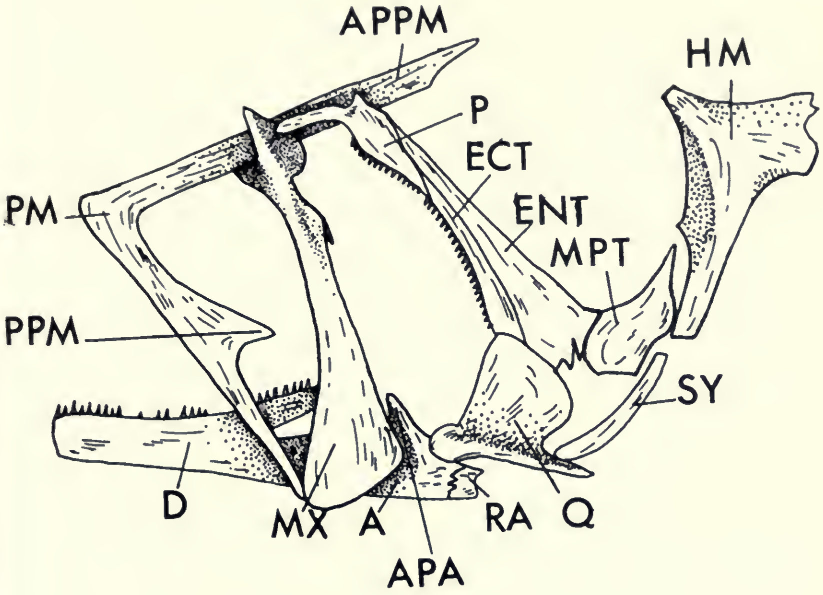

FIG. 12. Lateral view of oromandibular region of *Nandus nebulosus*. A, angular; APA, ascending process of angular; APPM, ascending process of premaxilla; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; HM, hyomandibular; MPT, metapterygoid; MX, maxilla; P, palatine; PM, premaxilla; PPM, postmaxillary process of premaxilla; Q, quadrate; RA, retroarticular; SY, symplectic.

the body of the prevomer. Posteriorly, the parasphenoid ends in an interdigitating suture with the basioccipital. No posterior opening of the myodome has been found in this area.

SUSPENSORY APPARATUS

As in most percoids, this unit is a functional triangle. The three angles are represented by the craniohyomandibular, palatocranial, and quadratomandibular joints. The posteroventral surface of this triangle serves as the site of origin of the adductor mandibulae muscles. The craniohyomandibular joint is a synovial joint, allowing lateromedial movements. The palatocranial joint is composed of two articular surfaces of the palatine and two articular surfaces of the prefrontal-lateral ethmoid complex in *Nandus*. In other nandids the palatine is connected to the prefrontal by a strong ligament. The palatocranial articulation is very mobile in all nandids except *Nandus*. When opening the mouth the suspensory apparatus rotates laterally around a longitudinal axis through the length of the cranio-

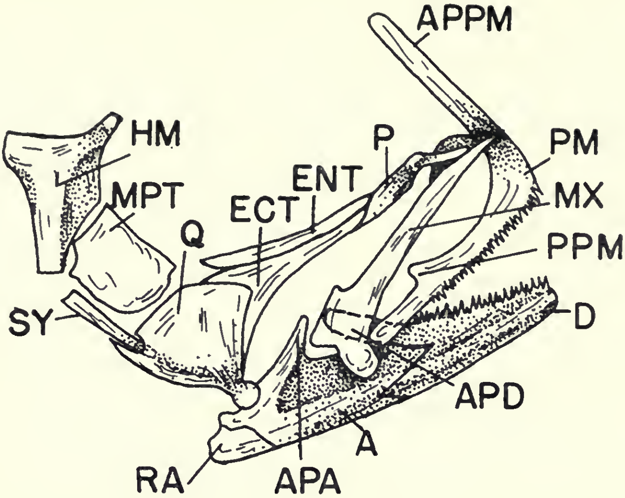

FIG. 13. Latetal view of oromandibular region of *Afronandus sheljuzkoi.* A, angular; APA, ascending process of angular; APD, ascending process of dentary; APPM, ascending process of premaxilla; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; HM, hyomandibular; MPT, metapterygoid; MX, maxilla; P, palatine; PM, premaxilla; PPM, postmaxillary process of premaxilla; Q, quadrate; RA, retroarticular; SY, symplectic.

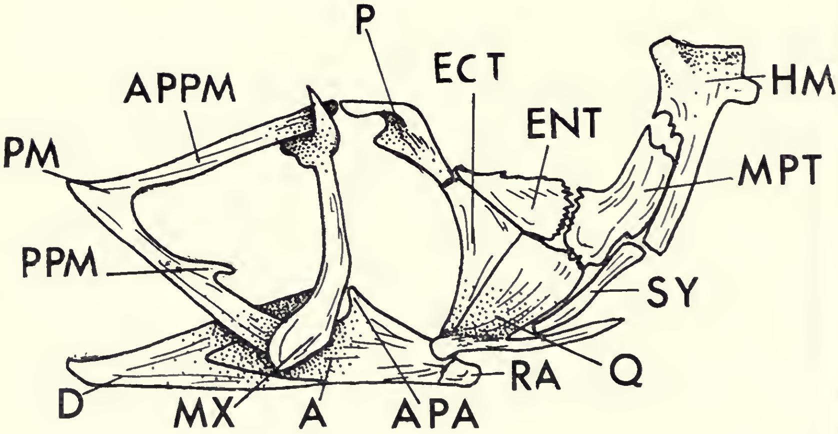

FIG. 14. Lateral view of oromandibular region of *Polycentrus schomburgkii.* A, angular; APA, ascending process of angular; APPM, ascending process of premaxilla; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; HM, hyomandibular; MPT, metapterygoid; MX, maxilla; P, palatine; PM, premaxilla; PPM, postmaxillary process of premaxilla; Q, quadrate; RA, retroarticular; SY, symplectic.

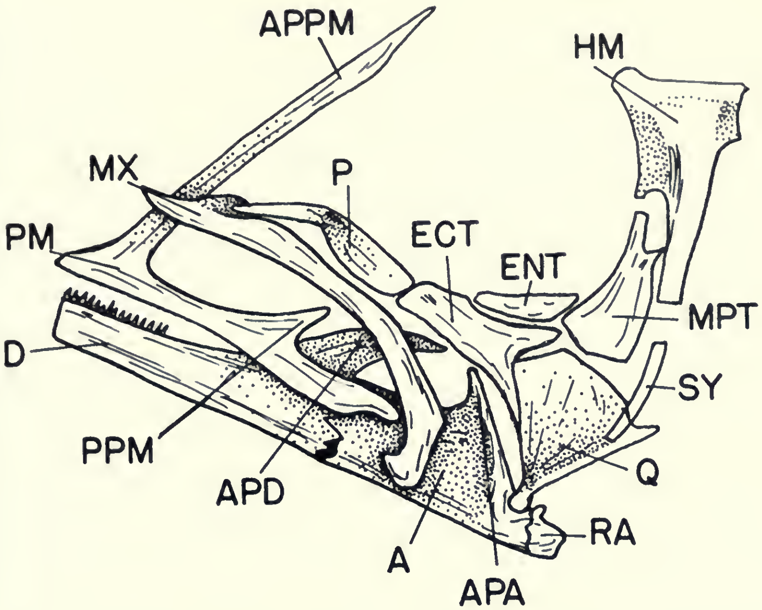

Fig. 15. Lateral view of oromandibular region of *Polycentropsis abbreviata*. A, angular; APA, ascending process of angular; APD, ascending process of dentary; APPM, ascending process of premaxilla; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; HM, hyomandibular; MPT, metapterygoid; MX, maxilla; P, palatine; PM, premaxilla; PPM, postmaxillary process of premaxilla; Q, quadrate; RA, retroarticular; SY, symplectic.

hyomandibular joint, so that the third angle, the quadratomandibular joint, is moved laterally. The quadratomandibular joint is essentially an euarthroidal saddle joint.

The suspensory apparatus is composed of eight bones: the hyomandibular, preopercular, palatine, ectopterygoid, entopterygoid, metapterygoid, symplectic, and quadrate.

The shape of the *hyomandibular* is very uniform in nandids. Two articular heads are apparent on the dorsal surface (Figs. 12–16: HM). The anterior one is a rounded head, directed anterodorsally and lodged in a rounded socket of the sphenotic. The posterior head is elongate and straight in a lateral view. It is accommodated in a shallow, longitudinal groove of the pterotic. The body of the hyomandibular is quadrangular. Ventrally, the hyomandibular gives rise to a long symplectic process. Posteriorly, the bone is differentiated into a rounded knob, which forms a ball and socket joint with a depression on the medial surface of the opercular. The anterior

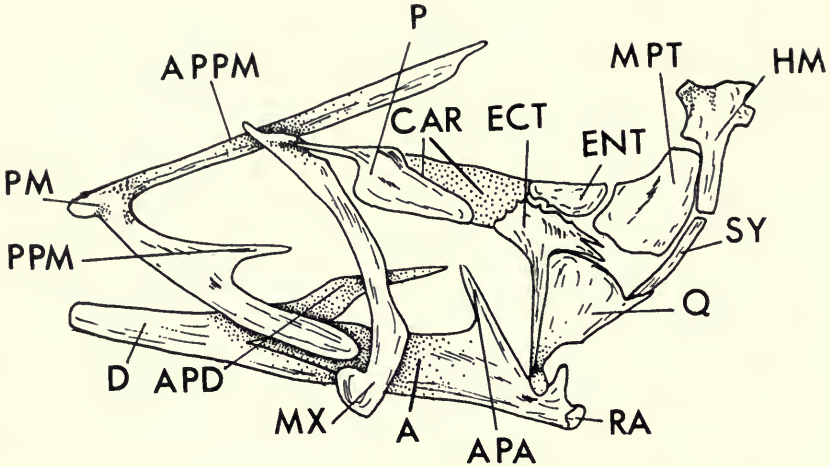

FIG. 16. Lateral view of oromandibular region of *Monocirrhus polyacanthus*. A, angular; APA, ascending process of angular; APD, ascending process of dentary; APPM, ascending process of premaxilla; CAR, cartilaginous joint between palatine and pterygoid; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; HM, hyomandibular; MPT, metapterygoid; MX, maxilla; P, palatine; PM, premaxilla; PPM, postmaxillary process of premaxilla; Q, quadrate; RA, retroarticular; SY, symplectic.

surface is differentiated into a spine that meets with a similar projection of the metapterygoid. In all nandids the metapterygoid is joined to the symplectic process of the hyomandibular.

The *symplectic* (Figs. 12–16: SY) is a slightly curved bone with a convex ventral border connecting the symplectic process of the hyomandibular with the quadrate. In *Polycentropsis* and *Monocirrhus* the symplectic is vertical (Figs. 15, 16).

The *quadrate* is a large triangular bone bearing a transverse condyle for the mandible at its ventral angle (Figs. 12–16: Q). The medial surface of the quadrate possesses a distinct fossa to house the symplectic bone. The fossa is horizontal in *Nandus, Afronandus,* and *Polycentrus*. In *Polycentropsis* and *Monocirrhus* the fossa is vertical in position. The bone articulates with the ectopterygoid and entopterygoid dorsally in *Nandus* and *Polycentrus*. In *Afronandus, Polycentropsis,* and *Monocirrhus* the entopterygoid does not join the quadrate. The connection between quadrate and metapterygoid is cartilaginous. The position of the quadrate in *Polycentropsis* and *Monocirrhus* is rather unique. The bone has rotated into a vertical position (Figs. 15, 16). The anteroventral position of the condyle, as found in *Nandus, Afronandus,* and *Polycentrus* has shifted into a

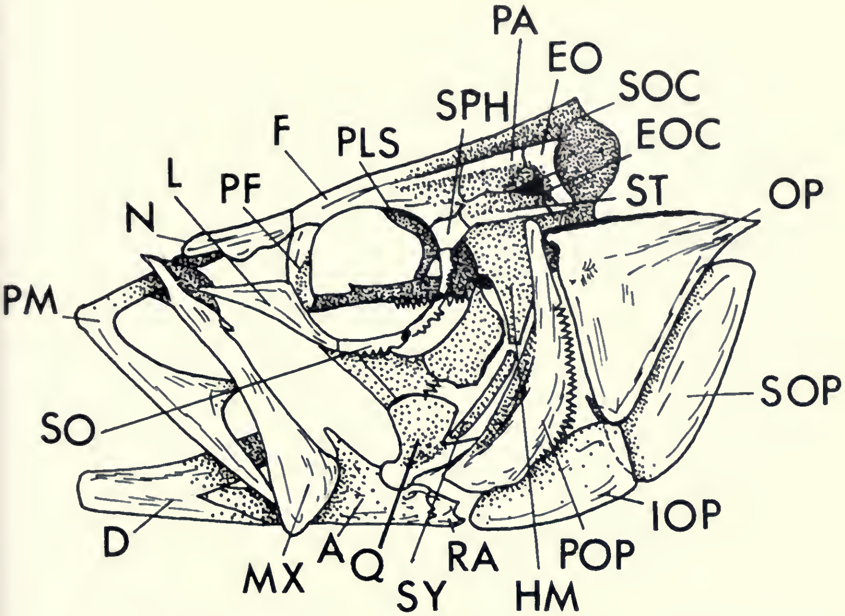

FIG. 17. Lateral view of intact skull of *Nandus nebulosus*. A, angular; D, dentary; EO, epiotic; EOC, exoccipital; F, frontal; HM, hyomandibular; IOP, interopercular; L, lachrymal; MX, maxilla; N, nasal; OP, opercular; PA, parietal; PF, prefrontal; PLS, pleurosphenoid; PM, premaxilla; POP, preopercular; Q, quadrate; RA, retroarticular; SO, circumorbital; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, pterotic; SY, symplectic.

midventral position. The preopercular fits in a groove on the posteroventral edge of the process forming the ventral border of the fossa for the symplectic.

The *preopercular* is functionally associated with the suspensory apparatus. The anterolateral surface serves as the origin of the adductor mandibulae muscles. The preopercular is ligamentously connected with the hyomandibular, symplectic, and quadrate. The motions of the preopercular are independent of the elements of the opercular apparatus. The preopercular undergoes the same movements as those of the suspensory apparatus. The preopercular of nandids (Figs. 17–21: POP) possesses characteristically a very short horizontal limb, except in *Afronandus,* which has a relatively well-developed horizontal arm (Fig. 18). The anterior edge is concave. The posterior margin is convex. The only non-serrated preopercular is found in *Monocirrhus* (Fig. 21). The pattern of serrations of the preopercular varies in the different genera. In *Nandus* the serration extends in a continuous band from the level of the ventral border of

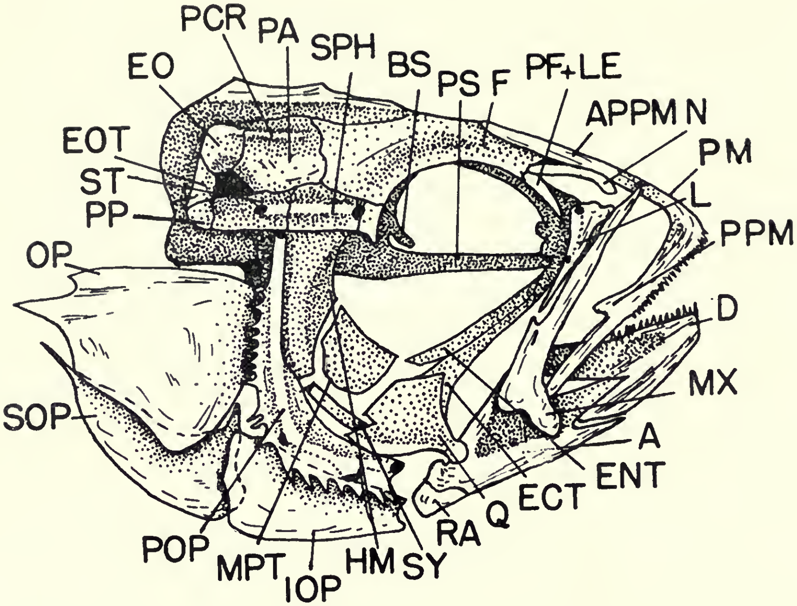

FIG. 18. Lateral view of intact skull of *Afronandus sheljuzkhoi*. A, angular; APPM, ascending process of premaxilla; BS, basisphenoid; D, dentary; ECT, ectopterygoid; ENT, entopterygoid; EO, epiotic; EOT, exoccipital; F, frontal; HM, hyomandibular; IOP, interopercular; L, lachrymal; MPT, metapterygoid; MX, maxilla; N, nasal; OP, opercular; PA, parietal; PCR, parietal crest; PF+LE, prefrontal-lateral ethmoid complex; PM, premaxilla; POP, preopercular; PP, intercalary; PPM, postmaxillary process of premaxilla; PS, parasphenoid; Q, quadrate; RA, retroarticular; SOP, subopercular; SPH, sphenotic; ST, pterotic; SY, symplectic.

of the orbit to the bend of the bone (Fig. 17). In *Afronandus* the spines extend along nearly the entire posterior margin. The ventral border of the horizontal limb is distinctly serrated with the spines directed anteroventrally. In *Polycentropsis* the serration is weakly developed and restricted around the angle of the bone and the horizontal limb (Fig. 20). In *Polycentrus* the serration is restricted to the ventral border of the horizontal limb (Fig. 19).

The *metapterygoid* possesses a slender projection directed toward a similar process on the symplectic process of the hyomandibular (Figs. 12–16: MPT). The metapterygoid is joined with the entopterygoid in *Nandus, Polycentrus,* and *Afronandus,* while an additional connection with the ectopterygoid has been found in *Polycentropsis* and *Monocirrhus.* A large cartilaginous plate represents the junction between quadrate and metapterygoid.

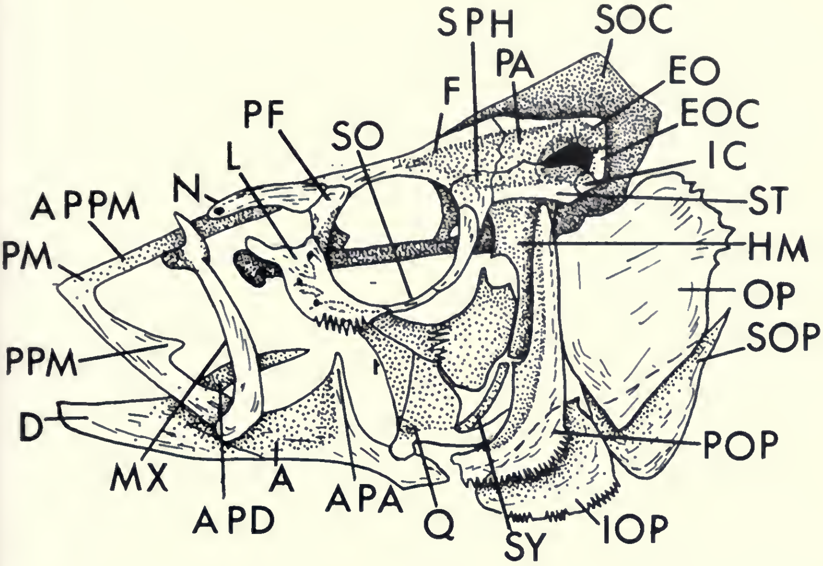

FIG. 19. Lateral view of intact skull of *Polycentrus schomburgkii*. A, angular; APA, ascending process of the angular; APD, ascending process of the dentary; APPM, ascending process of premaxilla; D, dentary; EO, epiotic; EOC, exoccipital; F, frontal; HM, hyomandibular; IC, intercalary; IOP, interopercular; L, lachrymal; MX, maxilla; N, nasal; OP, opercular; PA, parietal; PF, prefrontal; PM, premaxilla; POP, preopercular; PPM, postmaxillary process of premaxilla; Q, quadrate; SO, circumorbital; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, pterotic; SY, symplectic.

The *entopterygoid* in *Nandus* and *Afronandus* is an elongate bone extending from the body of the palatine bone to the anterior margin of the metapterygoid (Figs. 12, 13: ENT). It is joined to the palatine and ectopterygoid by a long, straight suture. The entopterygoid of *Polycentrus* is less extensive (Fig. 14). Dorsally it reaches the ventral corner of the palatine. The suture between entopterygoid and ectopterygoid is straight but rather short. In *Polycentropsis* and *Monocirrhus* the entopterygoid is reduced to a small bone wedged in between the metapterygoid and ectopterygoid (Figs. 15, 16). It has lost its association with the palatine.

The *ectopterygoid* possesses villiform teeth on its oral surface in *Nandus*. In all other genera the teeth are lacking (Figs. 12–16: ECT). A prominent posterior process embracing the anterodorsal corner of the quadrate separates the entopterygoid from the quadrate in *Polycentropsis* and *Monocirrhus*. The posterior process is lacking in the other genera. The ectopterygoid is joined to the palatine except in

Monocirrhus, which exhibits a very unique condition among teleosts. A large, flexible, cartilaginous block is interposed between the palatine, entopterygoid, and ectopterygoid (Fig. 16). This cartilaginous plate gives the palatine great mobility independent of the remaining elements integrated into the suspensory apparatus.

The oral surface of the *palatine* bears villiform teeth in *Nandus.* However, teeth are absent in the other genera. Anterodorsally, the palatine gives rise to a long, slender maxillary process that is closely associated with the head of the maxilla (Figs. 12–16: P). No special articular processes have been found except in *Nandus,* which possesses two special articular processes for articulation with similar processes of the lateral ethmoid-prefrontal complex (Fig. 12). In all other nandid genera the palatine is connected to the prefrontal by a prominent craniopalatine ligament (Fig. 44: CP).

OPERCULAR APPARATUS

Functionally, the preopercular belongs to the suspensory apparatus, because it serves as the origin of the adductor mandibulae muscles and its motions correspond with those of the suspensory apparatus and are independent of those of the opercular, interopercular, and subopercular. Inclusion of the preopercular in the opercular apparatus (e.g., Patterson, 1964) is, therefore, based on purely morphological reasons, without functional justification.

The opercular apparatus is complete and contains three bones.

The *opercular* is triangular. The posterodorsal corner is produced into a prominent spine in *Nandus, Polycentropsis,* and *Afronandus* (Figs. 17, 18, 20: OP). *Monocirrhus* and *Polycentrus* possess a variable number (2–7) of indistinct spines (Figs. 19, 21). The anterior border of the opercular is straight in *Nandus, Afronandus,* and *Polycentopsis,* and convex in *Polycentrus* and *Monocirrhus.* The facet that articulates with the knob-like opercular process of the hyomandibular is large and concave. The joint is synovial and of the ball-and-socket type.

The *subopercular* is ligamentously connected to the opercular. The dorsomedial margin is slightly overlapped by the opercular. A pointed, slender process extends dorsally medial to the opercular from its anterodorsal corner. The posterodorsal corner is produced into a slender process except in *Nandus* (Figs. 17–21: SOP).

The *interopercular* is somewhat elliptical (Figs. 17–21: IOP). The margins are not serrate, except in *Polycentropsis* (Fig. 20), *Polycen-*

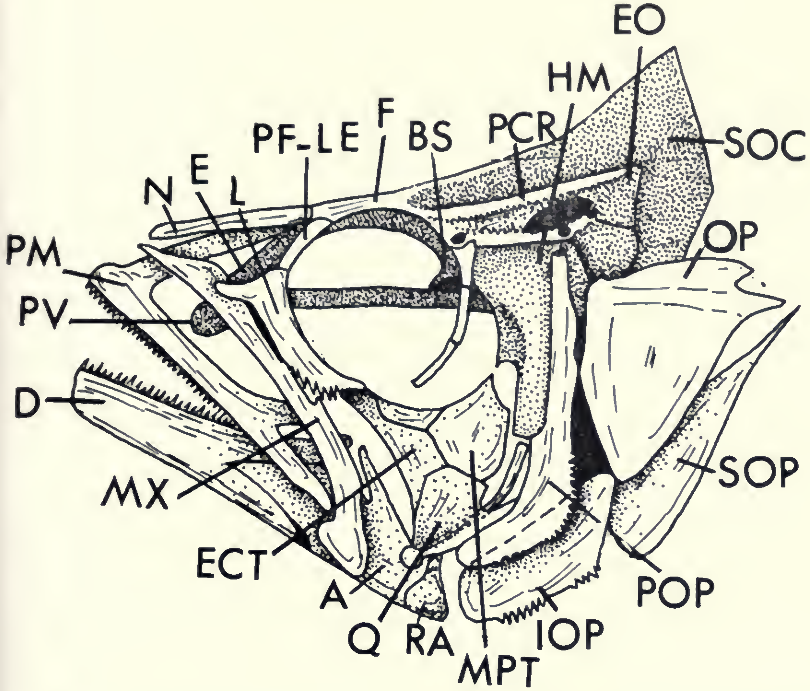

FIG. 20. Lateral view of intact skull of *Polycentropsis abbreviata*. A, angular; BS, basisphenoid; D, dentary; E, ethmoid; ECT, ectopterygoid; EO, epiotic; F, frontal; HM, hyomandibular; IOP, interopercular; L, lachrymal; MPT, metapterygoid; MX, maxilla; N, nasal; OP, opercular; PCR, parietal crest; PF–LE, prefrontal-lateral ethmoid complex; PM, premaxilla; POP, preopercular; PV, prevomer; Q, quadrate; RA, retroarticular; SOC, supraoccipital; SOP, subopercular.

trus (Fig. 19), and sometimes in *Nandus* (Khandelwal, 1965). The interopercular is characteristically connected by distinct ligaments to the opercular posterodorsally and to the mandible anteriorly (Figs. 29, 32, 33: IOL, IOPL). The subopercular is not interposed between interopercular and opercular. Rotating movements of the opercular are therefore directly transferred to the interopercular without the subopercular as an intermediary. The interopercular is not connected to the preopercular. The interopercular moves freely anteroposteriorly, independent of the preopercular.

JAW APPARATUS

The jaw apparatus is suspended from the suspensory apparatus by the quadratomandibular joint. The upper jaw is connected to the

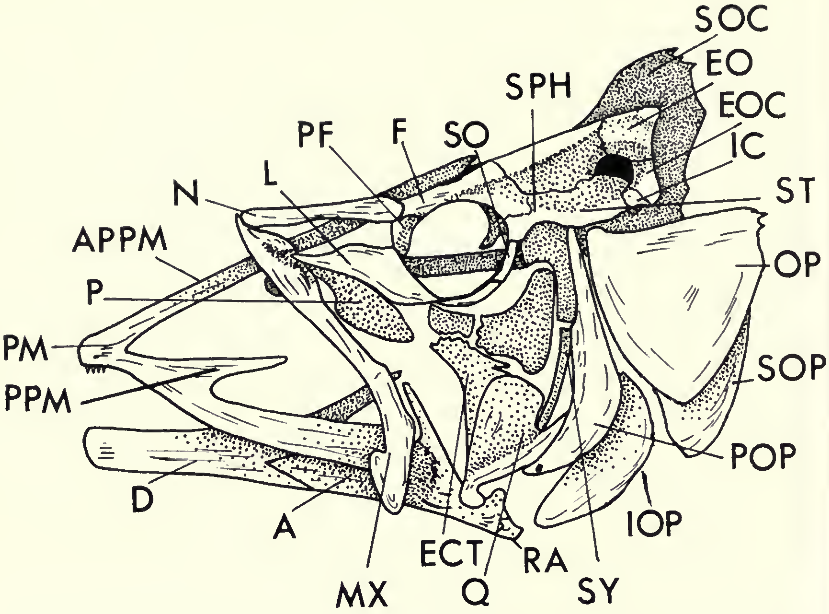

FIG. 21. Lateral view of intact skull of *Monocirrhus polyacanthus*. A, angular; APPM, ascending process of premaxilla; D, dentary; ECT, ectopterygoid; EO, epiotic; EOC, exoccipital; F, frontal; IC, intercalary; IOP, interopercular; L, lachrymal; MX, maxilla; N, nasal; OP, opercular; P, palatine; PF, prefrontal; PM, premaxilla; POP, preopercular; PPM, postmaxillary process of premaxilla; Q, quadrate; RA, retroarticular; SO, circumorbital; SOC, supraoccipital; SOP, subopercular; SPH, sphenotic; ST, pterotic; SY, symplectic.

neurocranium and suspensory apparatus by a complex system of ligaments and articular discs.

The mandible is very long. In *Monocirrhus* and *Polycentropsis* the total mandible length equals the total length of the neurocranium. The ratio of mandible length to neurocranial length in *Nandus* and *Afronandus* is, respectively, 6:7 and 3:4.

The mandible is composed of three bones: the dentary, angular (articular), and retroarticular.

The toothed *dentary* forms a very well-developed ascending (coronoid) process (Figs. 12–16: D, APD). The process is especially well differentiated in *Polycentropsis* and *Monocirrhus*. In the latter two genera (Figs. 15, 16) the ascending process gives rise to a posteriorly-directed projection as found in *Luciocephalus* (Liem, 1967a). Each dentary forms the anterior half of the mandible. The ascending processes of the dentary do not serve as the insertions of the adductor mandibulae muscles. The symphysis of the mandibular rami is mobile;

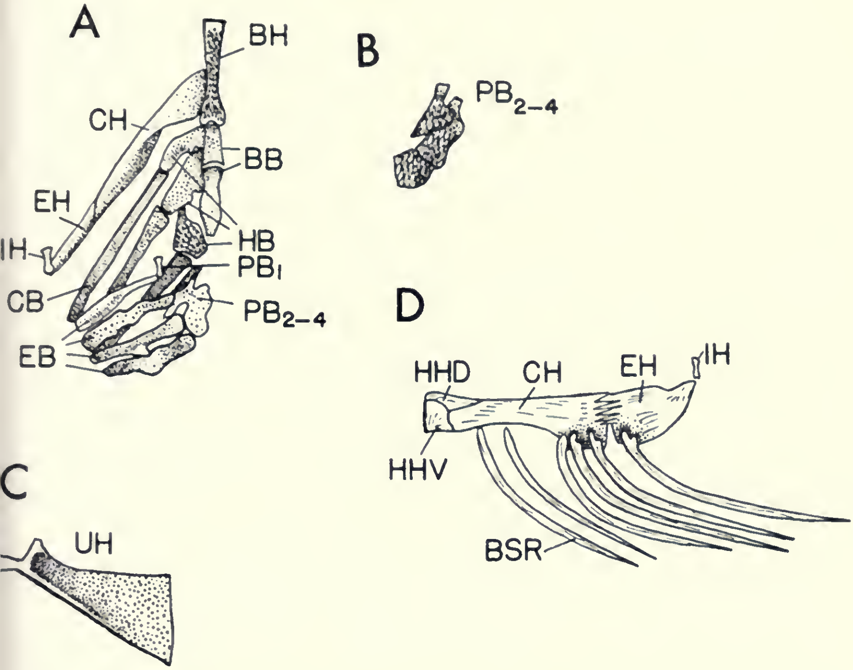

FIG. 22. *Nandus nebulosus*. A, Dorsal view of left half of hyobranchium. B, Ven-ral view of pharyngobranchials 2–4. C, Lateral view of urohyal. D, Lateral view of yoid apparatus. BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB, eratobranchial; CH, ceratohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; IHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB_1 and PB_{2-4} haryngobranchials; UH, urohyal.

The *angular* (articular) forms the posterior half of the mandible (Figs. 12–16: A). Anteriorly, the angular is rigidly lodged into a deep notch of the dentary. The anterodorsally-directed ascending process is moderately developed in *Nandus, Afronandus,* and *Polycentrus,* and highly developed in *Polycentropsis* and *Monocirrhus.* The ascending processes have no associations with either the adductor mandibulae muscles or the primordial ligament (Fig. 29). The angular possesses a fossa to receive the condyle of the quadrate with which it forms an euarthroidal joint.

The *retroarticular* forms that portion of the mandible posteroventral to the quadratomandibular joint. The suture between the retroarticular and angular is usually distinct (Figs. 12–16: RA). The interoperculomandibular ligament connects the retroarticular with the interopercular.

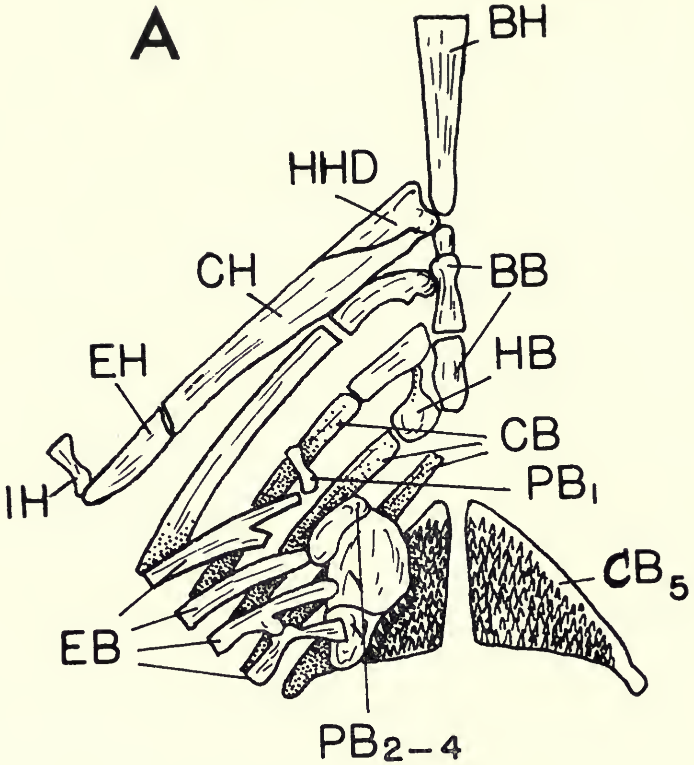

FIG. 23. *Afronandus sheljuzkhoi.* A, dorsal view of left half of hyobranchium; B, lateral view of hyoid apparatus; urohyal has been removed. BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB_5, ceratobranchial; CH, ceratohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; IH, interhyal; PB_{2-4}, pharyngobranchials.

The upper jaw of the jaw apparatus is composed of two bones: the premaxilla and maxilla.

The *premaxilla* consists of an elongate alveolar process bearing villiform teeth and a long ascending process (Figs. 12–16: PM, APPM). The ratio between the length of the ascending process and the neurocranial length in *Nandus, Afronandus, Polycentrus, Polycentropsis,* and *Monocirrhus* is, respectively, 1:2, 5:9, 1:2, 5:7, and 6:7.

Articular processes are absent in all nandid genera. The alveolar branch of the premaxilla possesses a postmaxillary process (Figs. 12–16: PPM) that is best developed in *Polycentropsis* and *Monocirrhus,* moderately developed in *Polycentrus* and *Nandus,* and least differentiated in *Afronandus.*

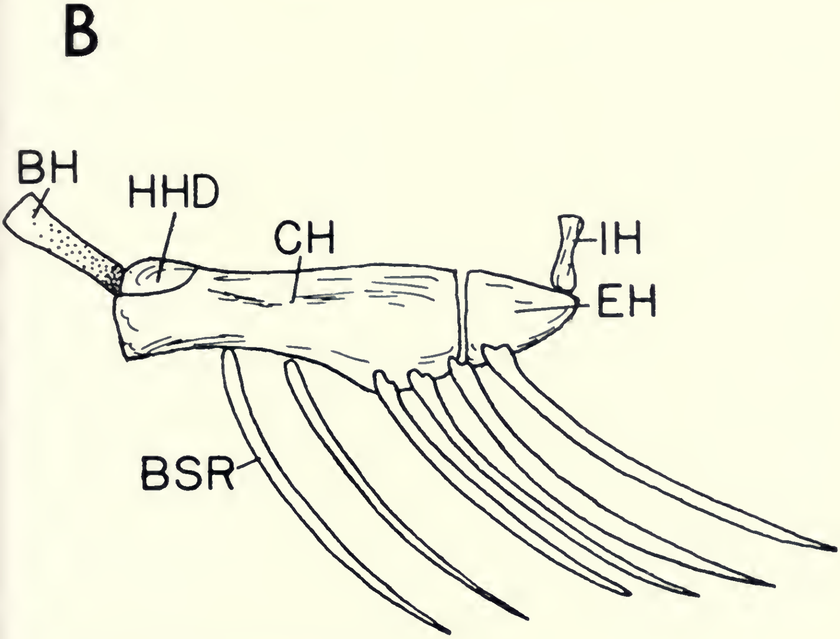

FIG. 23. *Afronandus sheljuskhai*, Continued.

The *maxilla* is large and elongate (Figs. 12-16: MX). The head of the maxilla is complex as in all percoids. The anterior median part of the head is the premaxillary condyle (Kayser, 1962; Alexander, 1967). The posterior median part of the maxillary head is the cranial condyle. The lateral part of the maxillary head terminates in a dorsal process that lies lateral to the ascending process of the premaxilla and medial to the maxillary process of the palatine. The morphology of the maxillary head is uniform among nandids. The body of the maxilla is stout and slightly curved; the anterior margin being concave. Ventrally, the maxilla expands and curves anteriorly in a rather sharp angle in all nandids except *Nandus* (Fig. 12).

HYOID APPARATUS

The hyoid apparatus consists of a V-shaped structure with the apex directed anteriorly. The two diverging limbs of the hyoid apparatus are suspended from the symplectic process of the hyomandibular by means of hour-glass-shaped interhyals. Each hyoid bar is composed of the epihyal, ceratohyal, and two hypohyals. Two unpaired elements, the basihyal and urohyal, project respectively anterodorsally and posteroventrally from the junction of the two hyoid bars. The hyoid apparatus can rotate up and down in the vertical plane; change the angle between the two hyoid bars; and shift forward and backward. A complex system of ligaments transmits the movements of the hyoid to the interopercular (Fig. 35: IHL).

The form of the hyoid apparatus is rather uniform in all nandid genera (Figs. 22-26).

The suspending elements are small rod-shaped *interhyals* (Figs. 22-25: IH). In lateral view the bone is hour-glass shaped. The interhyal is connected by cartilage and ligaments to the symplectic process of the hyomandibular and symplectic. Ventrally, the interhyal fits in a small fossa on the posterodorsal aspect of the epihyal. The joint is euarthroidal and a strong connective tissue capsule is always present. The interhyals are very long in *Monocirrhus* and *Polycentropsis* (Figs. 24, 25).

The *epihyal* is conical and the connection with the ceratohyal is by way of a strong interdigitating system of processes and fossae (Figs. 22-25: EH). The sixth branchiostegal ray articulates with the anteroventral corner of the epihyal.

The *ceratohyal* is the largest element (Figs. 22-25: CH). Both the dorsal and ventral margins are concave, if viewed from lateral. The posterior half of the bone is the deepest portion. The bone articulates with the first four branchiostegal rays. The fifth branchiostegal ray articulates with the hyoid bar at the interval between ceratohyal and epihyal.

The *dorsal* and *ventral hypohyal* are small elements that are firmly united to each other and to the ceratohyal (Figs. 22-25: HHD, HHV). The hypohyals form fossae to accommodate the basihyal and urohyal. The basihyal in *Nandus* and *Afronandus* is relatively short. The ratio between length of the basihyal to the length of the hyoid bar in *Nandus, Afronandus, Polycentrus, Polycentropsis,* and *Monocirrhus* is, respectively, 1:2, 1:2, 2:3, 3:4, and 4:5. In *Nandus* small villiform teeth cover the entire dorsal surface of the basihyal.

The *urohyal* is rigidly attached to the anterior ends of the hyoid bars. The bone possesses two processes: one anteriorly and one dorsally directed (Figs. 22, 24: UH; Fig. 25: URH). The urohyal is deep bodied in *Monocirrhus*. The lateral surface serves for the insertion of the sternohyoid muscles. A cross-section of the urohyal resembles an inverted Y.

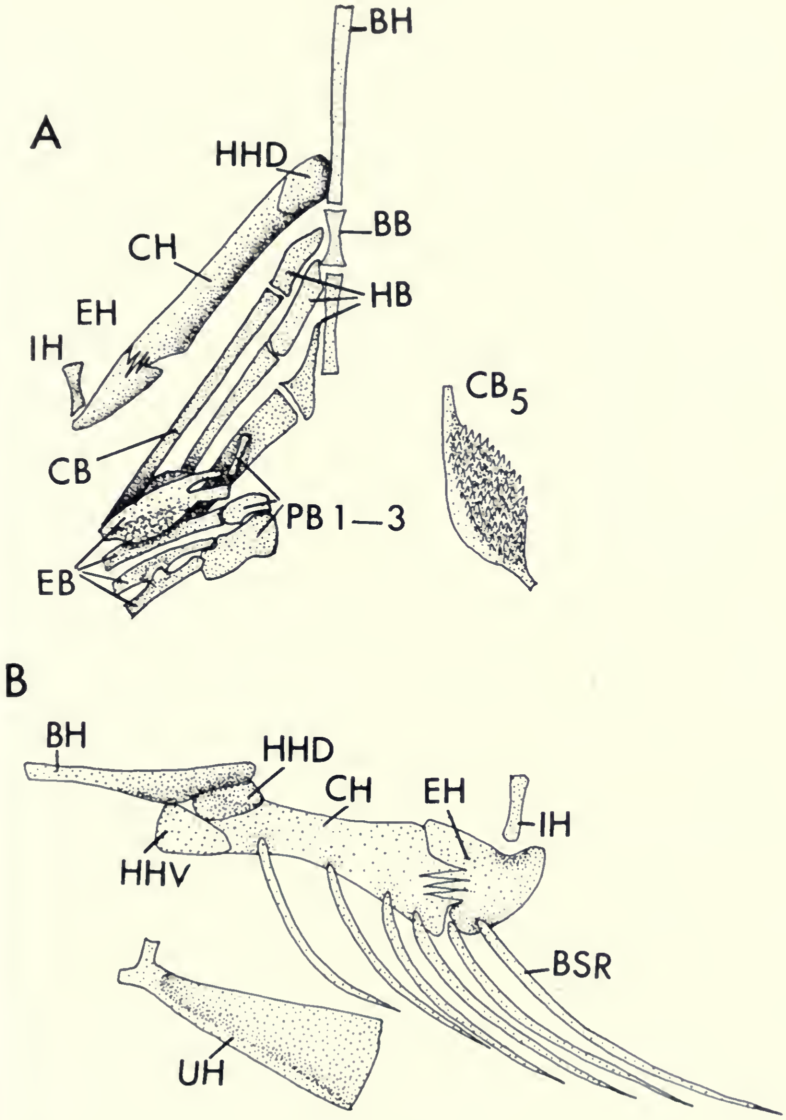

Fig. 24. *Polycentropsis abbreviata*. A, dorsal view of hyobranchium; B, lateral view of hyoid. BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB_5, ceratobranchial; CH, ceratohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB 1–3, pharyngobranchials; UH, urohyal.

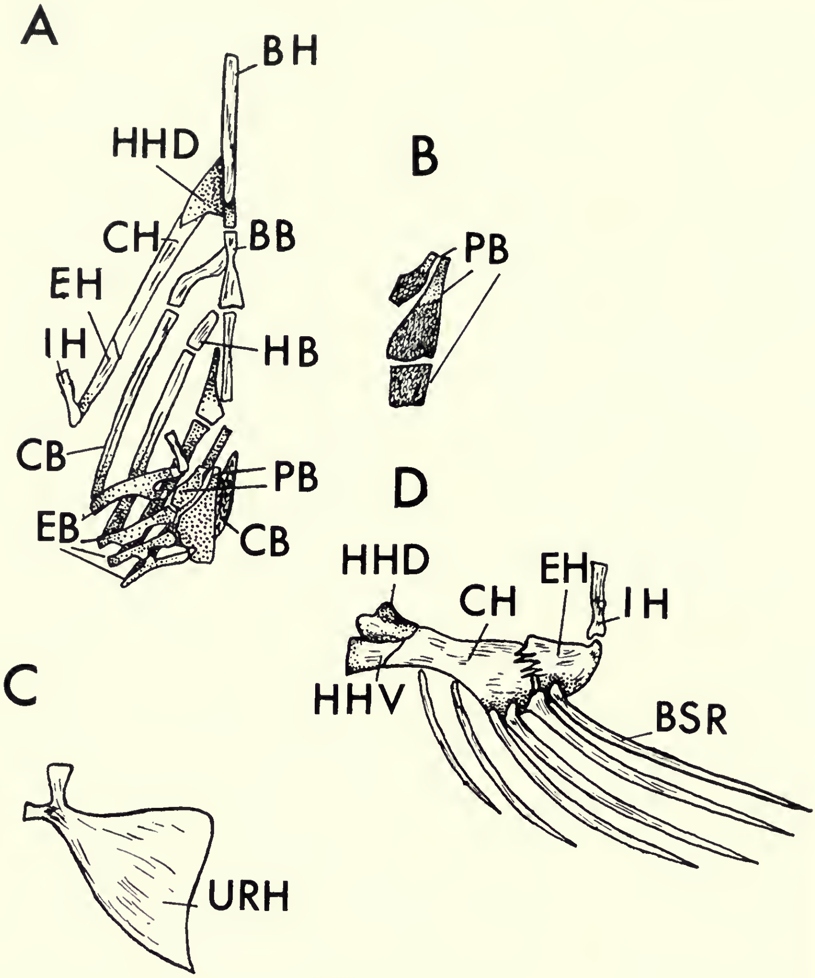

FIG. 25. *Monocirrhus polyacanthus.* A, dorsal view of left half of hyobranchium; B, ventral view of pharyngobranchials 2–4; C, lateral view of urohyal; D, lateral view of hyoid apparatus. BB, basibranchial; BH, basihyal; BSR, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; EB, epibranchial; EH, epihyal; HB, hypobranchial; HHD, dorsal hypohyal; HHV, ventral hypohyal; IH, interhyal; PB, pharyngobranchial; URH, urohyal.

Six *branchiostegal rays* are present, arranged in the characteristic percoid manner as described by Hubbs (1919) and McAllister (1968). In *Nandus* and *Afronandus* the dorsal heads of the posterior three and posterior four branchiostegal rays, respectively, are bifid (Figs. 22, 23: BSR).

BRANCHIAL APPARATUS

The branchial basket is closely associated with respiration since it bears the gills. However, it also is a very important feeding apparatus. Some branchial arches bear teeth and the associated muscles play a most important role during deglutition. The branchial apparatus is suspended from the neurocranium by the first pharyngobranchial. No other attachments with the neurocranium are found in nandids. The branchial arches are quite flexible, although no euarthroidal joints have been found between the bony elements. The bony elements are connected to each other by cartilage. The principle movements are: adduction and abduction within each arch involving the angle between the epibranchials and ceratobranchials; backward and forward movements of the second, third, and fourth pharyngobranchials and fifth ceratobranchial; rotating and sliding movements at the junctions between basibranchials and hypobranchials; and forward and backward movements of the branchial basket as one unit.

Three *basibranchials* are found in all nandids (Figs. 22–25: BB). The second basibranchial appears hour-glass shaped in a dorsal view. The last basibranchial is somewhat elongate. The first hypobranchial articulates with the second basibranchial, while the second hypobranchial is joined to the junction between the third and second basibranchials. The third hypobranchial is only loosely connected to the second basibranchial (Figs. 22–25).

Three pairs of *hypobranchials* are found in all nandids (Figs. 22–25: HB). The first hypobranchial is a slightly curved bone with the anterior margin convex and the posterior margin concave. The bone is more slender and more elongate in *Polycentropsis* and *Monocirrhus*. The second hypobranchial is rod-shaped. The third hypobranchial bears a distinct tooth plate on its dorsal surface in *Nandus*. It is toothless in the other genera. Anterolaterally, the third hypobranchial is produced into a long slender process (Figs. 22–25).

The first four *ceratobranchials* are elongate rod-like bones (Figs. 22–25: CB). The total length of the ceratobranchials increases if compared with the length of the neurocranium in the following order: *Afronandus, Nandus, Polycentrus, Polycentropsis,* and *Monocirrhus*. The fifth ceratobranchial bears a prominent tooth plate in all genera. Both anteriorly and posteriorly the fifth ceratobranchial is produced into distinct processes. The fifth ceratobranchial can move independently of the other elements of the branchial apparatus.

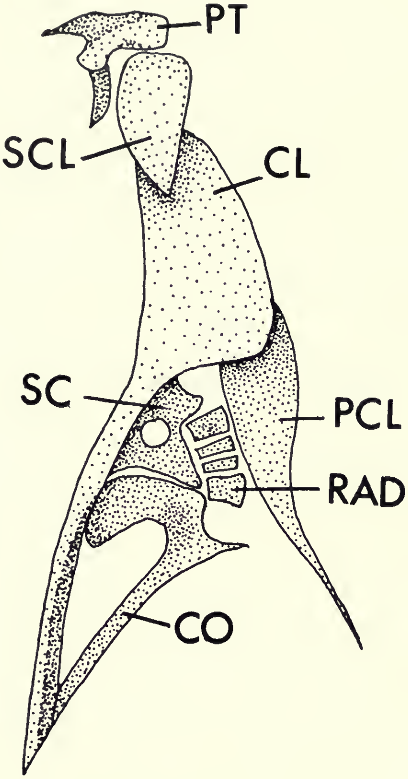

Fig. 26. Lateral view of left pectoral girdle of *Polycentropsis abbreviata*. CL, cleithrum; CO, coracoid; PCL, postcleithrum; PT, post-temporal; RAD, radial; SC, scapula; SCL, supracleithrum.

Four pairs of *epibranchials* are present (Figs. 22–25: EB). The first epibranchial is distinctly forked dorsally. In *Polycentropsis* the posterior and anterior margins of the first epibranchial are expanded into thin leaf-like bony plates resembling the modification so characteristic of the epibranchial of anabantoids (Fig. 24). It is possible that this expanded first epibranchial in *Polycentropsis* functions as an accessory air-breathing organ. The second epibranchial is a curved bone with a convex anterior margin. In *Monocirrhus* the posterior margin of the second epibranchial gives rise to a posteriorly-directed process. The third and fourth epibranchials are connected by, respectively, a posterior process and an anterior process (Figs. 22–25). The two processes overlap slightly. The last three epibranchials are joined to the last three pharyngobranchials.

The four *pharyngobranchials*[1] are of the general percoid type (Figs. 22–25: PB). The first pharyngobranchial is rod-like and articulates with the prootic by means of a ball-and-socket type joint. The second, third, and fourth pharyngobranchials are closely united into one upper pharyngeal bone. The second pharyngobranchial has an anteriorly-directed process. The dorsal surface of the upper pharyngeal bone possesses cristae for the insertion of muscles. Ventrally, the upper pharyngeal bone bears numerous villiform teeth.

PECTORAL GIRDLE

The pectoral girdle is suspended from the neurocranium by a mobile joint between supracleithrum and post-temporal (Fig. 26). The two halves are united ventrally in the cleithral symphysis. The pectoral girdle plays an important role in depressing the mandible. Ten bony elements make up one-half of the pectoral girdle.

The triangular *supracleithrum* is nearly vertical, with the apex directed ventrally (Fig. 26: SCL). Dorsally it has a distinct rounded articular facet for the ventral surface of the post-temporal. The ventral end of the supracleithrum articulates with the lateral face of the cleithrum.

The *cleithrum* is the largest element (Fig. 26: CL). It is sigmoid shaped. The dorsal vertical limb is somewhat expanded posteriorly. Dorsally, the cleithrum is fixed to the supracleithrum by a strong ligament that prevents sliding of the two bones. The ventral part, the horizontal limb, curves slightly forward and ventrally to form the posterior edge of the opercular opening. The endoskeletal girdle attaches on the posterior face of the horizontal limb.

The rectangular *scapula* is penetrated by a centrally-located, large scapular foramen (Fig. 26: SC). Its posterodorsal corner is produced into a blunt process. The posterior edge was covered by cartilage with which the three most dorsal radials articulate.

The *coracoid* articulates dorsally with the ventral edge of the scapula and anteriorly with the cleithral symphysis. Its posteroventral corner is produced into a long slender projection (Fig. 26: CO).

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[1] Recently, G. J. Nelson (Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates, Bull. Amer. Mus. Nat. Hist., 141, article, 4, 1969) has discussed the confusion concerning the nomenclature of the pharyngobranchials and associated toothplates. What I call upper pharyngeal bones or pharyngobranchials 3–4 are actually closely connected toothplates supported by infrapharyngobranchials 2 and 3 and toothplate of arch 4. Although the elements do not fuse to form a synostosis, they are firmly united by sutural connective tissue. Figures 23–25 are faithfully reproduced by camera lucida with a magnification at which the indistinct sutures are not visible.

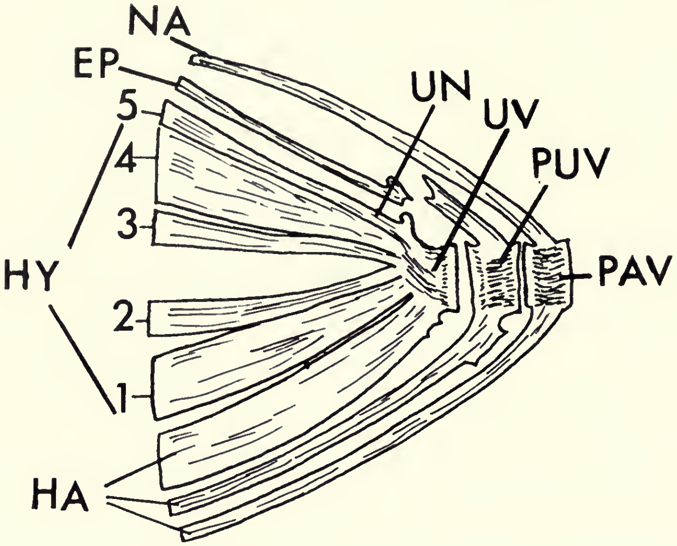

FIG. 27. Lateral view of caudal skeleton of *Afronandus sheljuzkoi*. EP, epural; HA, hemal arch; HY, hypural; NA, neural arch; PAV, antepenultimate vertebra; PUV, penultimate vertebra; UN, uroneural; UV, ultimate vertebra.

Four *radials* are present (Fig. 26: RAD). Three dorsal radials are articulating, by means of cartilage, with the posterior border of the scapula. The most ventral radial is the largest and articulates with the posterodorsal corner of the coracoid.

PELVIC GIRDLE

The two somewhat triangular *basipterygii* are united by a short median *symphysis* and a strong ligament near the bases of the fin rays. A prominent lateral ridge, the *rachis,* extends anterodorsally to become a spine that articulates with the medial surface of the cleithrum. Medial to this ridge arises a wing-like process, the *processus medialis anterior*. Originating from the posteromedial corner of the basipterygium are two processes, a slender anteriorly directed *processus medialis* and a posteriorly-directed, small, and blunt *processus medialis posterior*. The *processus lateralis* is an indistinct lateral projection of the basipterygium.

POSTCRANIAL AXIAL SKELETON

(Figure 28)

All Nandidae have 23 vertebrae (ultimate included). *Nandus* and *Afronandus* have 13 precaudal and 10 caudal vertebrae, while

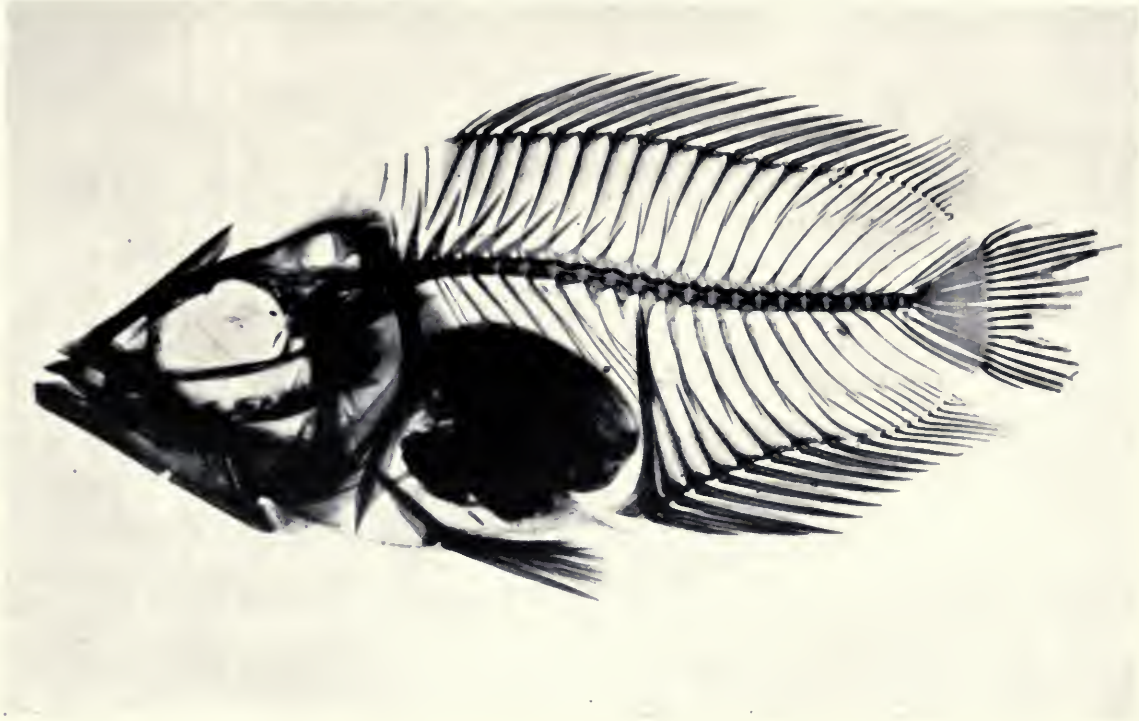

FIG. 28. Photograph of lateral view of skeleton of *Polycentropsis abbreviata* (cleared and stained) specimen. See text for explanation. (Photo by W. M. Winn.)

Table 2.—Some Meristic Characters of the Postcranial Skeleton of the Nandidae.

Species	Inter-neurals	Pterygiophores		Ribs	
		dorsal	anal	pleural	epipleural
Nandus nebulosus	3	24	8	9	11
Nandus nandus	3	24	8	9	11
Afronandus sheljuzkhoi	3	24	9	9	—
Polycentrus schomburgkii	3	24–25	16–17	8	7
Monocirrhus polyacanthus	3	27–28	23–24	8	4
Polycentropsis abbreviata	3	25–26	17–19	7–8	9

Polycentropsis, Polycentrus, and *Monocirrhus* have 10 precaudal and 13 caudal vertebrae (Fig. 28).

The *centra* of the first three precaudal vertebrae are shorter than those following. The first centrum is modified to form three articulations with the neurocranium in a pattern characteristic of percoids (Stokely, 1952; Dineen and Stokely, 1956). Distinct, narrow bridges on the lateral surfaces of the centra connecting the terminal convexities are present on all vertebrae except the first three. *Neural arches* are present and complete on all vertebrae except the ultimate. The first two neural spines are nearly perpendicular and interdigitate with the three interneurals. The *neural spines* of precaudals 3–9 are slanted posteriorly, except in *Nandus* and *Afronandus.* The neural spines of precaudal 10 and the first three caudals are again perpendicular. The transition between obliquely-slanted and perpendicular neural spines is sudden, except in *Nandus* and *Afronandus* in which all spines are obliquely slanted. The caudal neural spines in the posterior regions have progressively more slanted neural spines. The neural spines of the first nine precaudals are much heavier than the others. The "prezygapophyses" are short spines originating from the neural arch-directed anterodorsad. "Prezygapophyses" are not present on the first and ultimate vertebrae. In all vertebrae, except caudals 20 and 21, the "prezygapophyses" extend beyond the posterior margin of the preceding centrum. However, in *Nandus* and *Afronandus* the "prezygapophyses" are short, blunt, and indistinct.

"Postzygapophyses" are missing.

The *basapophyses* are present on precaudals 7, 8, and 9. Seven pairs of *pleural ribs* are present. The first four are attached directly to the centra, while the last three pairs articulate with the basapophyses. All precaudal vertebrae have epipleural ribs. Three *interneurals* are present. The first between neurocranium and first neural spine; the second between second and third neural spines; and the third between first dorsal pterygiophore and second neural spine in all nandids except *Nandus*. In *Nandus* interneurals 2 and 3 are interposed between the first and second neural spines, and the first two dorsal pterygiophores are between the second and third neural spines. The first *hemal arch* is directed straight ventrally, except in *Nandus* and *Afronandus* in which the first hemal arch is slanted obliquely posteroventrally. The hemal spines of the second, third, fourth, and fifth hemal arches extend farther ventrally than the others. The spine of the first hemal arch is the shortest and its anterior border is grooved to accommodate the posterior surface of the first ventral pterygiophore.

MEDIAN FIN SUPPORTS

The dorsal fin is supported by a variable number of pterygiophores (see Table 2). The first dorsal pterygiophore supports two spines. Posterior to the first dorsal pterygiophore the relationship between pterygiophores and spines and rays is one to one (Fig. 28). The first dorsal pterygiophore in *Polycentropsis* is between the second and third neural spines. The second and third pterygiophores are between the third and fourth neural spines. The next five pterygiophores interdigitate with the neural spines in a one-to-one ratio. No pterygiophore is between the ninth and tenth neural spines. The one-to-one ratio between dorsal pterygiophore and neural spine is re-established in the next four vertebrae. The ratio between dorsal pterygiophores and neural spines is two to one posterior to the fifteenth neural spine in *Polycentropsis* (Fig. 28). Conditions in other nandids vary slightly from this description of *Polycentropsis*.

The first ventral pterygiophore may represent a fusion of two. It carries two spines. The first pterygiophore is closely applied to the anterior surface of the hemal spine of the first caudal vertebra. The pterygiophore ascends dorsally to the base of the first hemal arch. The second ventral pterygiophore articulates with the posterior surface of the first pterygiophore. The third pterygiophore is applied to the posterior surface of the hemal spine of the first caudal vertebra. The ratio between the number of pterygiophores and neural spines varies intraspecifically.

CAUDAL FIN SUPPORTS

The caudal fin is supported by three vertebrae, although occasionally the antepenultimate vertebra does not get involved. One *epural* is always present (Figs. 27, 28). Five *hypurals* are attached to the ultimate vertebra. The *last hemal arch* is either attached or separated from the urostyle, the condition varies intraspecifically in nandids. The enlarged hemal arches of the antepenultimate and penultimate vertebrae serve for muscle attachments. The hypurals and hemal arch of the urostyle form a rigid plate for muscle attachments and articulation of caudal fin rays. Sixteen caudal fin rays are present in *Polycentropsis*. Dorsally, two small spines and ventrally one spine articulate with the caudal skeleton (Fig. 28). The nandid caudal skeleton differs significantly from that of *Pristolepis* (Patterson, 1968). The penultimate vertebra (second pre-ural centrum) of the Nandidae possesses a complete secondary neural spine (Fig. 28; Monod, 1968; Patterson, 1968), which is lacking in *Pristolepis* (Gosline, 1968). However, *Afronandus* represents a remarkable exception. It lacks the secondary neural spine (Fig. 27), which is present in all other nandids. The absence of the secondary neural spine on the second pre-ural centrum seems to indicate that *Afronandus* represents the most primitive nandid known.

Myology

The myology of the head region has been studied in all nandid genera except *Afronandus,* which was not available for dissection. This comparative and descriptive myology forms a basis for functional analysis and evolutionary synthesis described in the final portions of this paper. The muscles are described in relation to the associated functional units.

1. MUSCLES BETWEEN SUSPENSORY APPARATUS AND JAWS

All muscles of this category belong to the adductor mandibulae muscles. The nomenclature is that of Vetter (1874).

Nandus (Figs. 29–31: AM) possesses the most voluminous adductor mandibulae muscles that are differentiated into three distinct heads. *Pars A_1* is the most superficial head originating from the anterior border of the lower three-fourths of the preopercular. The fibers run parallel to insert on the long tendon, which extends between the tip of the cranial condyle of the maxillary and the fused tendons of pars A_2 and intramandibularis muscles (Fig. 29). *Pars A_2* lies deep compared to pars A_1. Pars A_2 originates from the entire anterior border of the preopercular. The fibers converge anteroventrally into a prominent bifid tendon. The ventral branch of the tendon (Fig. 30) attaches on the medial aspect of the mandible to the angular just ventral and anterior to the quadratomandibular joint. The anterior branch of the tendon is continuous with the tendon of the intramandibularis muscle. The *intramandibularis muscle* occupies the middle portion of the mandible (Fig. 31: IAM). The muscle fibers are attached to the dentary, not to the angular. The fibers converge to the common tendon of the adductor mandibulae complex. The intramandibularis and pars A_2 muscles form essentially one two-headed muscle intervened by a tendon in a similar way as the digastric of higher vertebrates.

In *Polycentrus* only two heads can be recognized among the adductor mandibulae muscles (Fig. 32: AM). One extensive, but sheetlike muscle, originates from the anterior margin of the preopercular.

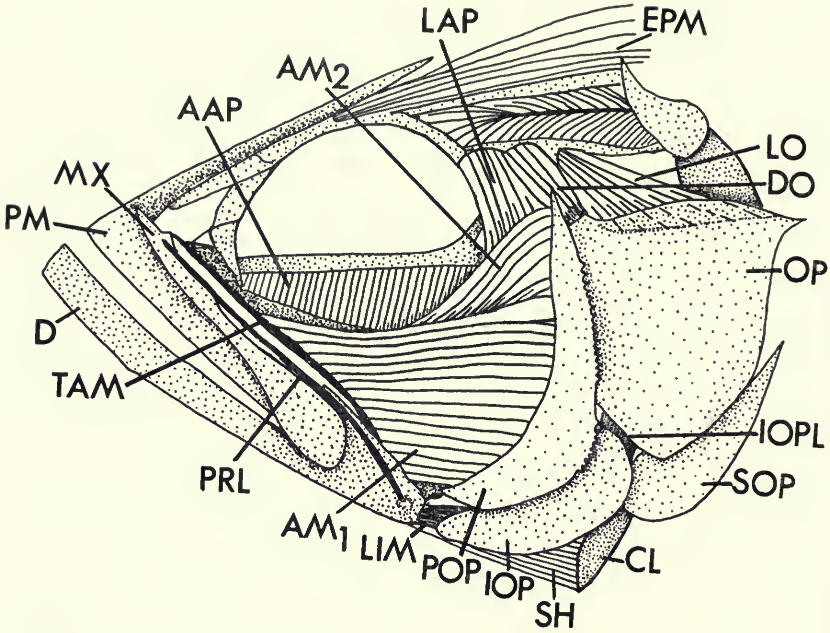

FIG. 29. Lateral aspect of cranial musculature of *Nandus nebulosus*. AAP, adductor arcus palatini muscle; AM_1, pars A_1 of adductor mandibulae muscle; AM_2, pars A_2 of adductor mandibulae muscle; CL, cleithrum; D, dentary; DO, dilatator operculi muscle; EPM, epaxial muscles; IOP, interopercular; IOPL, interoperculo-opercular ligament; LAP, levator arcus palatini muscle; LIM, interoperculomandibular ligament; LO, levator operculi muscle; MX, maxilla; OP, opercular; PM, premaxilla; POP, preopercular; PRL, primordial ligament; SH, sternohyoideus muscle; SOP, subopercular; TAM, tendon of pars A_1 of adductor mandibulae muscle.

The muscle fibers run parallel toward the tendon that runs from below the cranial condyle of the maxillary to the medial aspect of the angular just anterior and ventral to the quadratomandibular joint. No deeper muscle layer corresponding to pars A_2 of *Nandus* has been found in *Polycentrus*. A small pinnate intramandibularis muscle is present. Its tendon fuses with that of the adductor.

Monocirrhus and *Polycentropsis* resemble each other very closely in the configuration of the adductor muscles. As in *Polycentrus* the adductor mandibulae complex is composed of one extensive, sheet-like muscle of parallel fibers that originate from the anterior margin of the preopercular (Fig. 33: AM). The muscle mass seems relatively less than that of *Polycentrus*. The tendon of insertion runs between the base of the cranial condyle of the maxillary and the medial aspect of the angular, just anterior to the quadratomandibular joint. The *intramandibularis* is greatly reduced in *Monocirrhus* and *Polycentropsis*. A very few, but distinct, muscle fibers run from the dentary and converge to the tendon of the adductor mandibulae muscles (Fig. 34: IAM).

2. MUSCLES BETWEEN NEUROCRANIUM AND SUSPENSORY APPARATUS

The *adductor arcus palatini muscle* is uniform in form, extent, and topography throughout the nandids (Figs. 29, 32, 33: AAP). It is a thin muscle that forms part of the roof of the buccal cavity. Anteriorly, the muscle reaches the lateral ethmoid bone, while its posterior border extends to the anterior margin of the foramen of the internal carotid artery. The fleshy origin is the lateral aspect of the para-

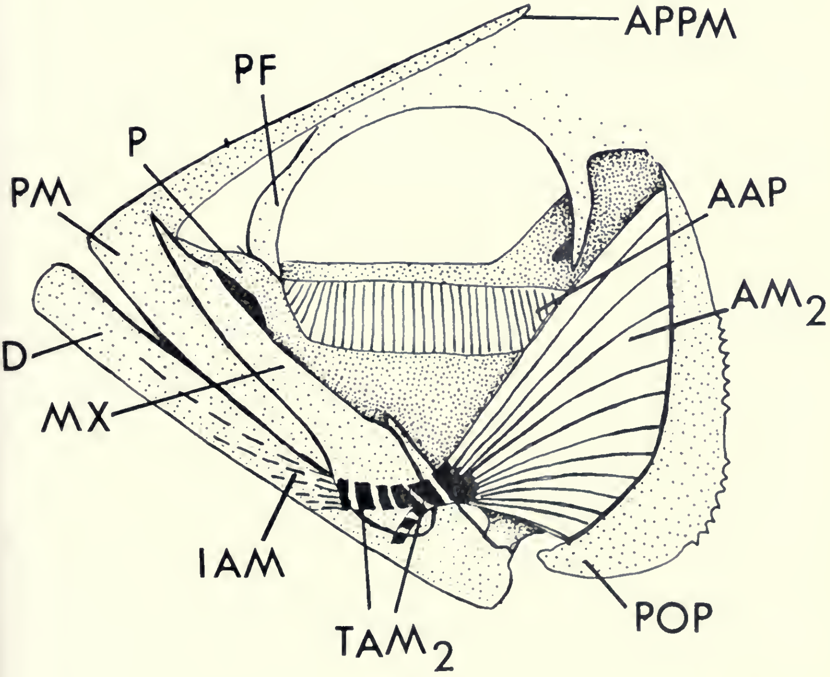

FIG. 30. Lateral view of deep adductor musculature of *Nandus nebulosus* after removal of A_1 portion of adductor mandibulae muscle. AAP, adductor arcus palatini muscle; AM_2, pars A_2 of adductor mandibulae muscle; APPM, ascending process of the premaxilla; D, dentary; IAM, intramandibularis portion of adductor mandibulae muscle; MX, maxilla; P, palatine; PF, prefrontal; PM, premaxilla; POP, preopercular; TAM_2, tendon of pars A_2 of adductor mandibulae muscle.

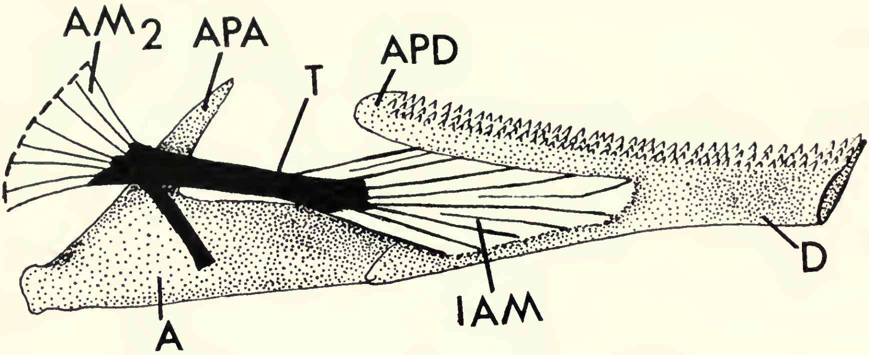

FIG. 31. Medial aspect of the mandible of *Nandus nebulosus*. A, angular; AM_2, pars A_2 of adductor mandibulae muscle; APA, ascending process of angular; APD, ascending process of dentary; D, dentary; IAM, intramandibularis portion of adductor mandibulae muscle; T, tendon between intramandibularis and pars A_2 of adductor mandibulae muscle.

sphenoid. The muscle fibers run parallel from this origin to the fleshy insertion on the medial surface of the dorsal rim of the entopterygoid and metapterygoid and symplectic process of the hyomandibular. The muscle has both a fleshy origin and insertion and is parallel-fibered. The muscle is best developed in *Nandus*.

3. MUSCLES BETWEEN NEUROCRANIUM AND OPERCULAR APPARATUS

The muscle of this group is involved in the motions of the opercular apparatus. The opercular can be abducted, adducted, and rotated.

The *dilator operculi muscle* originates from the fossa posterior to the postorbital process of the sphenotic (Figs. 29, 32, 33: DO). The muscle fibers converge on the process at the anterodorsal corner of the opercular. The tendinous insertion is on the lateral surface of the process. The muscle is relatively long and rectangular in *Nandus*. In *Polycentrus* the muscle is spindle shaped. *Polycentropsis* and *Monocirrhus* have rather short, fan-shaped dilator operculi muscles.

The *levator operculi* is a very prominent muscle in all nandids (Figs. 29, 32, 33: LO). It lies immediately posterior to the dilator operculi. The fibers originate from the lateral surface of the pterotic and diverge to the dorsal surface of the ridge, which is continuous with the opercular spine on the medial aspect of the opercular. The insertion on the dorsal ridge that is continuous with the opercular spine is fleshy. The origin is tendinous and much more restricted to the posterolateral corner of the pterotic in *Polycentropsis* and *Monocirrhus*.

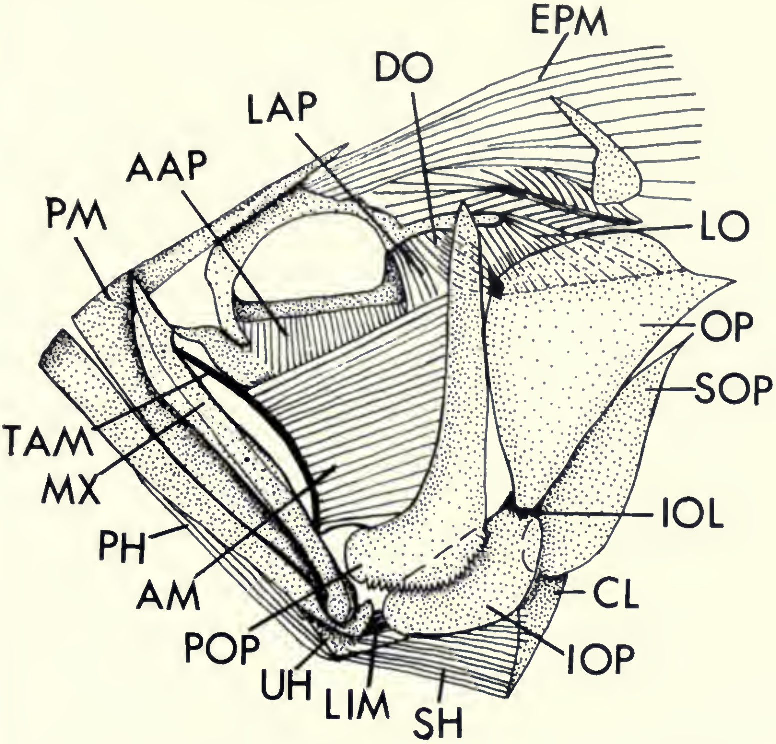

FIG. 32. Lateral aspect of cranial musculature of *Polycentrus schomburgkii*. AAP, adductor arcus palatini muscle; AM, adductor mandibulae muscle; CL, cleithrum; DO, dilatator operculi muscle; EPM, epaxial muscles; IOL, interoperculo-opercular ligament; IOP, interopercular; LAP, levator arcus palatini muscle; LIM, interoperculomandibular ligament; LO, levator operculi muscle; MX, maxilla; OP, opercular; PH, protractor hyoideus muscle; PM, premaxilla; POP, preopercular; SH, sternohyoideus muscle; SOP, subopercular; TAM, tendon of adductor mandibulae muscle; UH, urohyal.

In *Nandus* and *Polycentrus* the origin is more anteriorly located and fleshy.

The *adductor operculi* is a small parallel-fibered muscle that is closely associated with the insertion of the levator operculi. The fibers insert ventral to the insertion of the levator operculi. They originate from the prootic and run posterolaterally to the medial surface of the opercular. Both origin and insertion are fleshy.

4. VENTRAL MUSCLES OF THE HEAD

Profound differences have been found in the different nandid genera in respect to the protractor hyoid and sternohyoid muscles. The *intermandibularis muscle* is characteristically absent in the nandids.

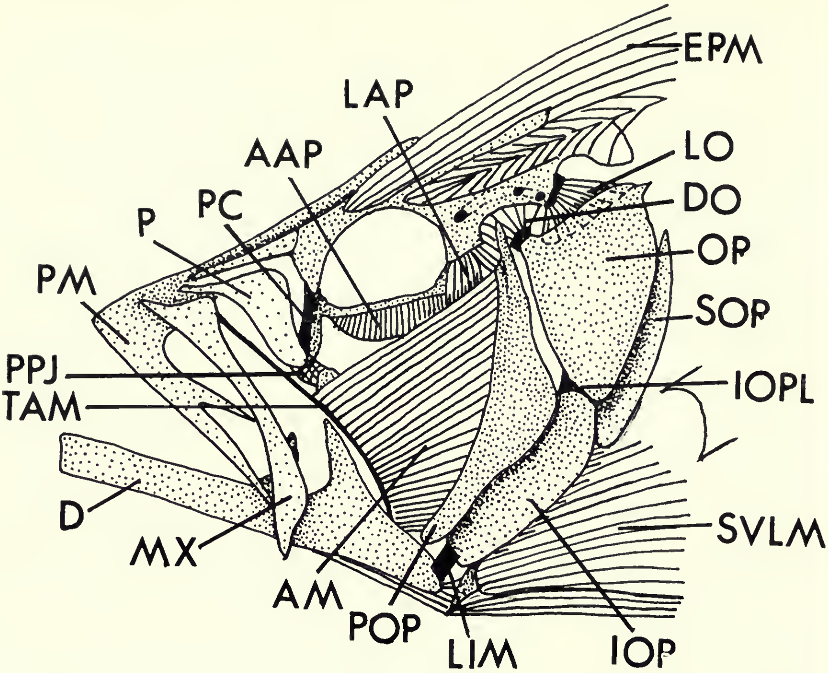

Fig. 33. Lateral view of cranial musculature of *Monocirrhus polyacanthus*. AAP, musculus adductor arcus palatini; AM, musculus adductor mandibulae; D, dentary; DO, musculus dilatator operculi; EPM, epaxial musculature; IOP, interopercular; IOPL, interoperculo-opercular ligament; LAP, musculus levator arcus palatini; LIM, interoperculomandibular ligament; LO, musculus levator operculi; MX, maxilla; OP, opercular; P, palatine; PC, palatocranial ligament; PM, premaxilla; POP, preopercular; PPJ, palatopterygoid joint; SOP, subopercular; SVLM, superficial ventrolateral body musculature; TAM, tendon of adductor mandibulae muscle.

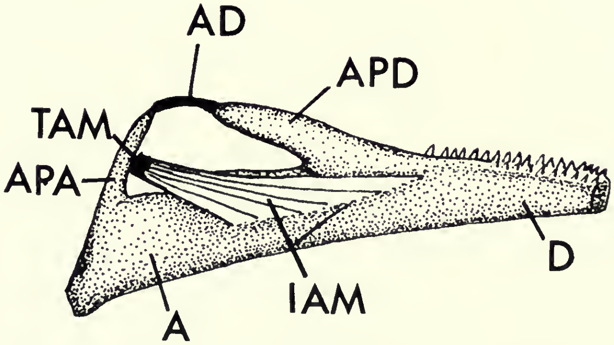

Fig. 34. Medial view of mandible of *Monocirrhus polyacanthus*. A, angular; AD, angulodental ligament; APA, ascending process of angular; APD, ascending process of dentary; D, dentary; IAM, intramandibular portion of adductor mandibulae muscle; TAM, tendon of adductor mandibulae muscle.

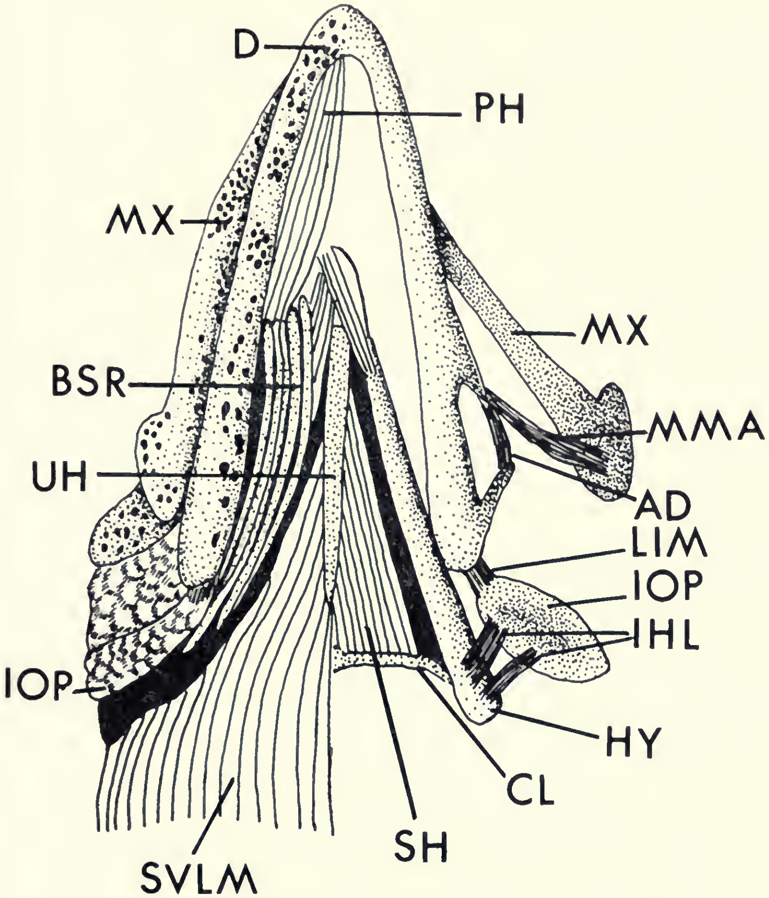

FIG. 35. Ventral aspect of ventral cranial musculature of *Nandus nebulosus*. Protractor hyoideus, branchiostegal rays, and superficial ventrolateral body musculature have been removed from left side. Ligaments on left side are exposed. AD, angulodental ligament; BSR, branchiostegal rays; CL, cleithrum; D, dentary; HY, hyoid; IHL, interoperculohyoid ligaments; IOP, interopercular; LIM, interoperculomandibular ligament; MMA, medial maxillomandibular ligament; MX, maxilla; PH, protractor hyoideus muscle; SH, sternohyoideus muscle; SVLM, superficial ventrolateral body musculature; UH, urohyal.

The *protractor hyoideus* is also known as the geniohyoid. In *Nandus* the muscle is large and spindle shaped (Fig. 35: PH). It originates from the posterior surface of the anterior angle of the mandible. Posteriorly, the muscle fibers insert on the lateral surface of the hyoid between the second and third branchiostegal rays. No muscle fibers are attached to the ventral hypohyals.

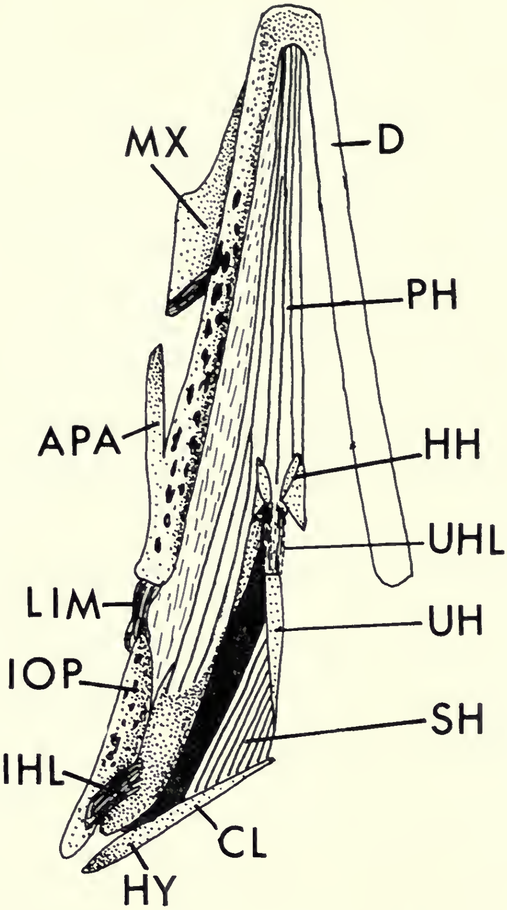

FIG. 36. Ventral aspect of head musculature of *Monocirrhus polyacanthus*. Muscles, hyoid, and cleithrum of left side are not shown. APA, ascending process of angular; CL, cleithrum; D, dentary; HH, hypohyal; HY, hyoid; IHL, interoperculohyoid ligament; IOP, interopercular; LIM, interoperculomandibular ligament; MX, maxilla; PH, protractor hyoideus muscle; SH, sternohyoideus muscle; UH, urohyal; UHL, urohyalohypohyal ligament.

In *Monocirrhus* and *Polycentropsis* the protractor hyoideus is much more elongate and parallel fibered (Fig. 36: PH). Its origin from the posterior surface of the angle of the mandibular rami is more restricted. The fibers of the lateral half of the muscle run posterolaterally to insert on the lateral surface of the ceratohyal. *Polycentrus* resembles *Monocirrhus*, but the fibers are shorter.

The superficial layer of the *ventrolateral body musculature* extends anteriorly, inserting on the urohyal (Fig. 35: SVLM). The muscle fibers insert on the lateral surface of the posterior half of the urohyal. Most fibers of the ventrolateral body musculature insert on the pectoral girdle, but the ventromedial part overlies the cleithra to converge on the urohyal. This superficial layer of the ventrolateral body musculature apparently aids in retracting and depressing the hyoid apparatus. It can be considered a synergist of the sternohyoid muscle.

The *sternohyoideus muscle* lies deep to the superficial layer of the ventrolateral muscles. In all nandids the muscle is a simple sheet of parallel fibers. The fleshy origin is from the anterior margin of the horizontal limb of the cleithrum and the fleshy insertion is the entire lateral surface of the urohyal (Figs. 35, 36: SH). In lateral view the muscle is narrow in *Nandus* and very broad in *Monocirrhus* and *Polycentropsis* (Figs. 35, 36). The broadening is the result of an increased number of muscle fibers made possible by the greater depth of the urohyal and the less acute angle between the horizontal and vertical limbs of the cleithrum.

Tendons and pinnation are absent in the sternohyoideus muscles.

5. EPAXIAL MUSCLES

The *epaxial muscles* extend far anteriorly on the dorsal surface of the neurocranium. The anterior border of the epaxial muscles reaches a level corresponding to the middle of the orbit. The configuration and extent of the epaxial muscles in relation to the neurocranium are uniform among the nandids (Figs. 29, 32, 33: EPM).

Two components, the lateral and medial, can be recognized in the epaxial muscles associated with the neurocranium. The medial component extends farther anteriorly than the lateral and occupies the fossa bordered laterally by the parietal crest and medially by the supraoccipital crest and the margin of the rostral fossa. The muscle fibers run parallel and insert in the fossa of the neurocranium musculously. Neither tendons nor any pinnation have been found in the medial component of the epaxial muscles. The lateral component of the epaxial muscle occupies the fossa bordered laterally by the margins of the pterotic and sphenotic and medially by the parietal crest. The muscle fibers converge posteriorly on a median longitudinal tendon (Figs. 29, 32, 33). The muscle fibers are attached to the walls of the fossa formed by the parietal crests and lateral walls of the pterotic and sphenotic. The attachment to the bones is fleshy.

Posteriorly, the lateral and medial components of the epaxial muscles are continuous with the epaxial muscles of the body.

Afronandus possesses the least developed neurocranial epaxial musculature. The extent of insertion on the neurocranium is the least extensive among nandids. However, both lateral and medial components are differentiated in *Afronandus*.

6. MUSCLES BETWEEN NEUROCRANIUM AND PECTORAL GIRDLE

A prominent muscle between the neurocranium and pectoral girdle is present in all nandids. In general, this muscle is regarded as a derivative of the interarcuales dorsales series. Dietz (1914) named this muscle the *cephaloscapularis*. In accordance with Kayser (1962) and Karrer (1967) the muscle is called the *trapezius*. The trapezius originates from the ventral surface of the pterotic just posterior to the craniohyomandibular joint and inserts on the anterior surface of the dorsal half of the vertical limb of the cleithrum (Figs. 37, 38: TR). The insertion is tendinous, and the fibers converge toward the insertion site. The most caudal fibers insert just ventral to the junction between cleithrum and supracleithrum. The origin of the trapezius is just caudal to the origins of the adductor hyomandibularis and adductor operculi muscles.

7. MUSCLES OF THE BRANCHIAL APPARATUS

The muscles associated with the branchial apparatus are especially active during deglutition. The intrinsic branchial muscles, i.e., muscles that extend between two branchial elements, are reduced both in number and morphological differentiation in nandids. The *adductor arcuum branchialium muscles* are completely absent. The preponderance of parallel-fibered muscles is found in all nandids. The muscles are grouped according to major functional features, and this approach reflects neither ontogeny nor phylogeny. The rather unconventional grouping seems more meaningful in relation to the functions of functional units and couplings between the functional units. The nomenclature of the muscles is adopted from Kirchhoff (1958), Kayser (1962), and Karrer (1967), because of the functional basis on which their terminology is based.

8. MUSCLES BETWEEN BRANCHIAL APPARATUS AND NEUROCRANIUM

Three *levatores arcuum branchialium externi muscles* originate from the prootic just ventral and medial to the craniohyomandibular joint,

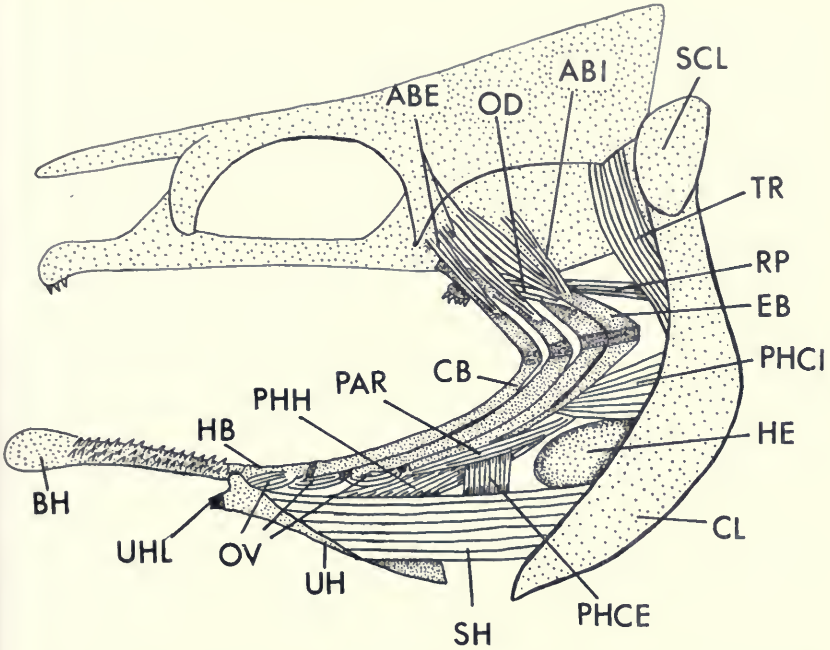

FIG. 37. Lateral aspect of branchial musculature of *Nandus nebulosus*. ABE, levator arcuum branchialium externus; ABI, levator arcuum branchialium internus; BH, basihyal; CB, ceratobranchial; CL, cleithrum; EB, epibranchial; HB, hypobranchial; HE, heart; OD, obliquus dorsalis; OV, obliquus ventralis; PAR, pharyngoarcualis; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PHH, pharyngohyoideus; RP, retractor ossium pharyngealium; SCL, supracleithrum; SH, sternohyoideus; TR, trapezius; UH, urohyal; UHL, urohyalohypohyal ligament.

and insert on the dorsolateral surfaces of the first and second epibranchials and at the junction of the third and fourth epibranchials. The latter two bones articulate by, respectively, a posterior and an anterior process (Figs. 22–25: EB). All external levators are parallel-fibered, strap-like muscles (Figs. 37, 38: ABE). The origins are muscular, the insertions are either muscular or somewhat tendinous. In the adducted condition of the branchial arches the muscle fibers run mainly in an anteroposterior direction. The two anterior muscles are equally developed, while the third and most posterior one is always the most prominent. The latter may represent a complete fusion of two muscles.

Two spindle-shaped *levatores arcuum branchialium interni muscles* are present (Figs. 37, 38: ABI). The internal series is not as well developed as the outer one. The muscular origins are medial to those

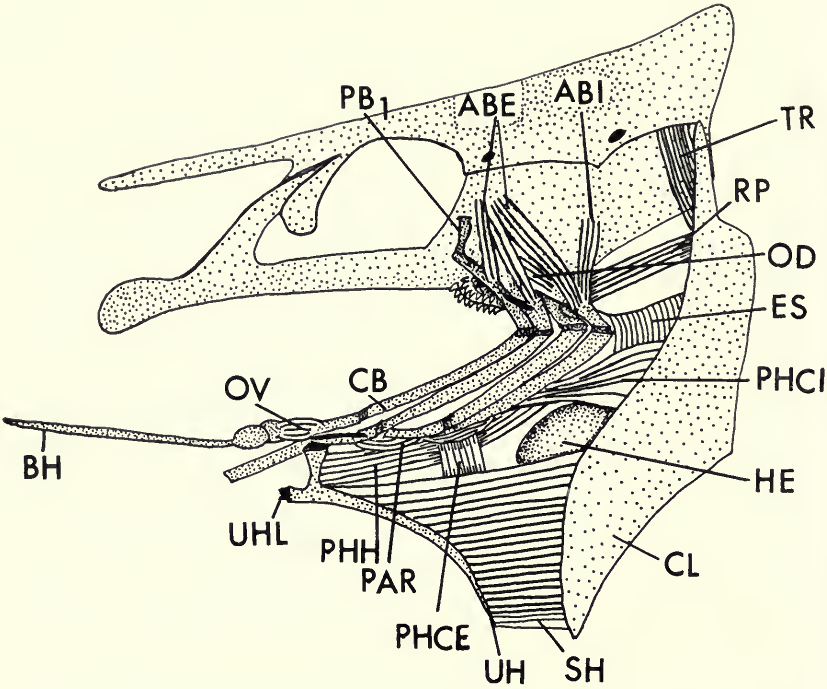

FIG. 38. Lateral aspect of branchial musculature of *Monocirrhus polyacanthus*. ABE, levator arcuum branchialium externus; ABI, levator arcuum branchialium posterior; BH, basihyal; CB, ceratobranchial; CL, cleithrum; ES, esophagus; HE, heart; OD, obliquus dorsalis; OV, obliquus ventralis; PAR, pharyngoarcualis; PB_1, first pharyngobranchial; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PHH, pharyngohyoideus; RP, retractor ossium pharyngealium; SH, sternohyoideus; TR, trapezius; UH, urohyal; UHL, urohyalohypohyal ligament.

of the external series. The first internal levator inserts on the dorsal surface of the second pharyngobranchial. The second inserts on the dorsal surface of the fourth pharyngobranchial.

The *levator posterior muscle* is present (Fig. 38: ABI).

9. MUSCLES BETWEEN BRANCHIAL APPARATUS AND HYOID APPARATUS

This group is represented by one muscle only, the *pharyngohyoideus* (the rectus communis of Edgeworth (1935) and Nelson (1967)), characteristic of all acanthopterygians. More primitive teleosts lack a muscle extending from the fifth ceratobranchial to the urohyal (Dietz, 1914). However, a homologue of this muscle is present in more primitive teleosts with different sites of origins and insertions according to Nelson (1967) who considers the pharyngohyoideus a derivative of the rectus of the fourth branchial arch. The pharyngohyoideus muscle is well developed in nandids (Figs. 37, 38: PHH). The muscle is parallel fibered and runs close to the median plane between the ventral surface of the toothed fifth ceratobranchial and the dorsal process of the urohyal. The height of the dorsal process of the urohyal (Figs. 22, 25) is directly correlated with the development of the pharyngohyoideus muscle. The best developed pharyngohyoideus is found in *Monocirrhus* and *Polycentropsis,* which have the highest dorsal process of the urohyal. The fiber direction is anteroposterior. Both insertion and origin are aponeurotic. In *Monocirrhus* each muscle has two bellies interrupted by a broad aponeurosis at the site where the pharyngohyoideus passes lateral to the pharyngocleithralis externus muscle. In morphology the pharyngohyoideus of *Monocirrhus* resembles the digastric of mammals.

The presence of a pharyngohyoideus muscle is directly correlated with the presence of the retractor ossium pharyngealium muscles in higher teleosts.

10. MUSCLES BETWEEN BRANCHIAL APPARATUS AND PECTORAL GIRDLE

Two well differentiated muscles between the branchial apparatus and pectoral girdle are uniformly present in nandids and other percoids. The *pharyngocleithralis muscle* (pharyngoclaviculares of Dietz (1914); coracobranchialis of Nelson (1967)) is differentiated into two widely separated heads (Figs. 37, 38: PHCI, PHCE).

The *pharyngocleithralis externus muscle* originates from the anterior tip of the horizontal arm of the cleithrum and runs straight dorsally to insert on the ventral surface of the fifth ceratobranchial. The strap-like muscle is parallel fibered. Both insertion and origin are aponeurotic. This division of the muscle runs near the median plane immediately anterior to the pericardium. The fiber direction is vertical (Figs. 37, 38: PHCE).

The second head, the *pharyngocleithralis internus,* originates much more dorsally from the anterior surface of the cleithrum. The rather extensive origin is just ventral to the insertion of the trapezius muscle (Figs. 37, 38: PHCI). The muscle fibers converge anteriorly on a tendon that is inserted on the ventral surface of the caudal tip of the fifth ceratobranchial. The fiber direction is anteroposterior. The muscle is situated just dorsal to the pericardium. The insertion is tendinous, while the origin is fleshy. The muscle seems most elongate in *Monocirrhus.*

11. INTRINSIC BRANCHIAL MUSCULATURE

All intrinsic branchial muscles are adductors, although in a few instances adduction in one part of the branchial apparatus may result in abduction of another region. The configuration and size of the intrinsic branchial muscles are quite uniform in the nandids. The nomenclature of the intrinsic branchial musculature has been unstable and various authors have proposed different names for the same muscles. The nomenclature of Dietz (1914) has been adopted since it corresponds with that of other authors (Kirchhoff, 1958; Kayser, 1962; Karrer, 1967), who have employed a functional rather than an ontogenetic-phylogenetic approach. The term attachments is substituted for origin and insertion because in all cases there is great mobility of the bony elements on either side of the muscle, making it impossible to distinguish between origin and insertion.

As in all acanthopterygians only one *obliquus dorsalis muscle* is present. The well-developed, spindle-shaped muscle (Figs. 37, 38: OD) extends between the dorsal surface of the medial edge of the third pharyngobranchial and the dorsal process of the third epibranchial. Both attachments are tendinous.

Two *transversus dorsalis muscles* are differentiated (Fig. 39: TDA, TDP). The transversus dorsalis anterior muscle (the obliquo-transversus muscle of Dietz (1914)) extends between the first and second epibranchials of either side. The attachments are tendinous and the muscle is spindle shaped in a dorsal view. Just posterior to this muscle is a weaker-developed, parallel-fibered, transversus dorsalis posterior muscle extending between the dorsomedial margins of the posterior pharyngobranchials. Both attachments are ligamentous. The transversus dorsalis posterior muscle fuses insensibly with the *constrictor pharyngis muscle,* which underlies the retractor pharyngealium muscles. The constrictor pharyngis muscle embraces the dorsal part of the esophageal entrance (Fig. 39: CPH). The border line between the constrictor pharyngis and sphincter oesophagii muscles is inconspicuous.

The *adductor arcuum branchialis muscles* are absent.

Three *obliqui ventrales muscles* are present (Figs. 37, 38: OV). They span the ventral cartilaginous junction between the ceratobranchial and hypobranchial of one arch. The muscles are fan shaped

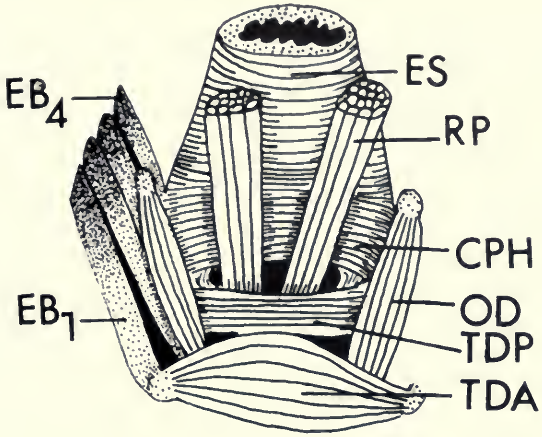

FIG. 39. Dorsal aspect of dorsal branchial musculature of *Monocirrhus polyacanthus*. Pharyngobranchials not shown; levators arcuum branchialium externus and internus removed; epibranchials from right side not drawn in. CPH, constrictor pharyngis muscle; EB_1 and EB_4, epibranchial 1 and 4; ES, esophagus; OD, obliquus dorsalis muscle; RP, retractor ossium pharyngealium; TDA, transversus dorsalis anterior muscle; TDP, transversus dorsalis posterior muscle.

and of more or less equal size. The attachments are tendinous. The fourth branchial arch lacks an obliquus ventralis muscle.

A large *pharyngo-arcualis muscle* is found as a derivative of the interarcualis series. The elongate muscle extends between the ventral surface of the third basibranchial to the ventral surface of the fifth ceratobranchial (Figs. 37, 38: PAR). Both attachments of the spindle-shaped muscle are tendinous.

The small *interarcualis muscle* extends between the third hypobranchial and the fourth ceratobranchial.

The *transversi ventrales muscles* are present on the fourth and fifth branchial arches. Both muscles are parallel fibered and have tendinous attachments. The transversus ventralis of the fourth arch extends between the medial margins of the fourth ceratobranchials, while that of the fifth arch bridges the gap between the fifth ceratobranchial of either side.

12. MUSCLES BETWEEN BRANCHIAL APPARATUS AND VERTEBRAL COLUMN

The *retractor ossium pharyngealium muscles* are well developed and cylindrical (Figs. 37–39: RP). The tendinous insertion is on the dorsal surface of the posterior margin of the last pharyngobranchial. The tendinous origin of the muscles included the caudolateral edges of the second and third vertebrae.

13. MUSCLES OF MEDIAN FINS

Both the spiny and soft rays are supported by the pterygiophores, which lie in the median plane in a strong vertical sheet of connective tissue. The joint between the spiny ray and its pterygiophore prevents lateral motions of the spiny portion of the fin. The joint between soft ray and pterygiophore is of the ball-and-socket type, allowing the soft part of the median fins to perform lateromedial, anteroposterior, and rotational movements. The transition from hinge type to the ball-and-socket type of pterygiophore-ray joints is rather gradual. Accordingly, the musculature responsible for the lateromedial movements of the rays is progressively better developed in the posterior regions. The inclinatores muscles are absent from the spiny portion of the fin.

The following paired muscles are associated with each soft ray:

(a) The *inclinatores muscle* originates from an aponeurosis that lies between the epaxial muscles and neural spines. The muscle is inserted on the lateral surface of the base of the fin ray; (b) The *erectores muscle* lies deep to the inclinatores. The erectores muscle originates from the pterygiophore and the vertical median sheet of connective tissue. The tendinous insertion is attached to the anterior surface of the base of the fin ray; (c) The *depressor muscle* lies posterior to the erectores muscle of the same ray. It also originates from the pterygiophore and the median vertical connective tissue sheet. The tendinous insertion is on the posterior surface of the base of the ray. The erectors and depressors are especially well developed in the spiny rays.

Each ray possesses its own set of muscles and nerves. Although the fin is moved in a coordinated way, each fin ray is independent. Injury to the fin membrane, or removal of several rays does not affect the movement of the fin as a whole (Baerends and Baerends-van Roon, 1950).

The movement of the spiny rays is restricted to a median vertical plane. The rays can be erected at any intermediate angle for variable durations. The major function of the median fins is to prevent rolling during swimming and gliding movements (Harris, 1938). The lateral movements of the soft parts of the median fins are controlled by the inclinatores muscles. The exact function of the undulatory movements, especially evident in *Monocirrhus,* is not known in the nandids. No major differences have been found between the nandid genera in respect to the architecture of the median fins.

14. MUSCLES OF THE CAUDAL FIN

The caudal architecture is very uniform in nandids and resembles that of "generalized" percoids.

The *deltoid flexor tendon* is not as well developed as in other percoids (Nursall, 1963; Nag, 1967). The only developed part is dorsal to the horizontal septum. Distally, the tendon is inserted on the central caudal fin rays of the dorsal half of the fin. Anteriorly, the flexor tendon becomes associated with the deep fascia of the superficial flexor muscles. The deltoid flexor tendon serves to reinforce flexion of the tail. Its incomplete differentiation seems to indicate that strong flexion of the caudal fin plays a minor role in locomotion of the nandids.

The *superficial dorsal flexor muscle* (Fig. 40: SDF) is the special portion of the last myomere. The dorsal bundle inserts by tendons to the caudal fin spines and the first two dorsal rays. These tendons overlie the tendons to the first two dorsal rays of the hypochordal longitudinal muscle. The ventral half of the superficial dorsal flexor runs underneath the hypochordal longitudinal muscle to insert on the remaining caudal fin rays of the dorsal half of the fin.

The *superficial ventral flexor muscle* (Fig. 40: SVF) represents the hypaxial portion of the last myomere. The superficial dorsal and ventral flexors are not sharply separated. Distally, the superficial ventral flexor muscle inserts by means of an aponeurosis to all fin rays ventral to the horizontal septum.

The *supra-* and *infracarinalis muscles* are small, bridging in *Monocirrhus, Polycentropsis,* and *Polycentrus,* very narrow gaps between the bases of the soft dorsal and anal fins to the caudal fin.

The *hypochordal longitudinal muscle* is obliquely located, emerging from beneath the deep ventral flexor muscle (Fig. 40: HCL). The fleshy origin is from the surfaces of the first three hypurals. The insertions on the first four fin rays is tendinous.

The *deep dorsal flexor muscle* is deep to the superficial dorsal flexor. It originates from the antepenultimate, penultimate, and urostyle vertebrae and their neural arches. The muscle inserts by separate tendons to the more dorsal rays and by a common tendon to the more ventral rays. The insertion is deep to the hypochordal longitudinal muscle (Fig. 40: DDF).

The *deep ventral flexor muscle* is differentiated into three different subdivisions, although the demarcations are not always sharp. The origin is from the vertebral bodies and hemal arches of the antepenultimate, penultimate, and ultimate vertebrae. The insertion is by some separate tendons and broad aponeuroses to all the rays of the ventral half of the caudal fin (Fig. 40: DVF).

The *dorsal adductor muscle* seems to be missing in nandids.

The *interradial muscles* are well developed, especially toward the center of the fin (Fig. 40: IR). The fiber direction is oblique, running from an anterodorsal to a posteroventral position. The fibers are found between adjacent rays. The fibers are restricted between two successive rays. None of the fibers bypasses one or more rays.

The enlarged hemal arches of the antepenultimate, penultimate, and ultimate vertebrae and the hypurals serve as a support for the fin rays and origin of the caudal musculature. The joints between fin rays and hypurals are much more complex (Nursall, 1963) than previously recorded (Baerends and Baerends-van Roon, 1950). The joints are virtually synovial, allowing flexion, extension, abduction, adduction, and rotation. The functional role of the different muscles has been analyzed by Nursall (1963) and Nag (1967). Their interpretation is adopted here. Flexion, i.e., bending to one side, is accomplished by the superficial flexors, both dorsal and ventral flexors, and the hypochordal longitudinal muscles. The flexors of one side are the extensors of the other. Abduction is the result of contraction of the deep dorsal and ventral flexors, whereas the adductors are the hypochordal longitudinal muscles. Limited rotation takes place by the abductor, adductor, and some flexor muscles. The inter-radial muscles are the chief adductors of the caudal fin rays. The caudal fin is always spread and closed as a whole as described for the cichlids by Baerends and Baerends-van Roon (1950). The fin undulates by a longitudinal wave passing from dorsal to ventral as observed by Nursall (1963) in perciform fishes. The nandids often hover in the water without progression performing complex movements with the caudal fin, presumably through action of the inter-radials. The fin

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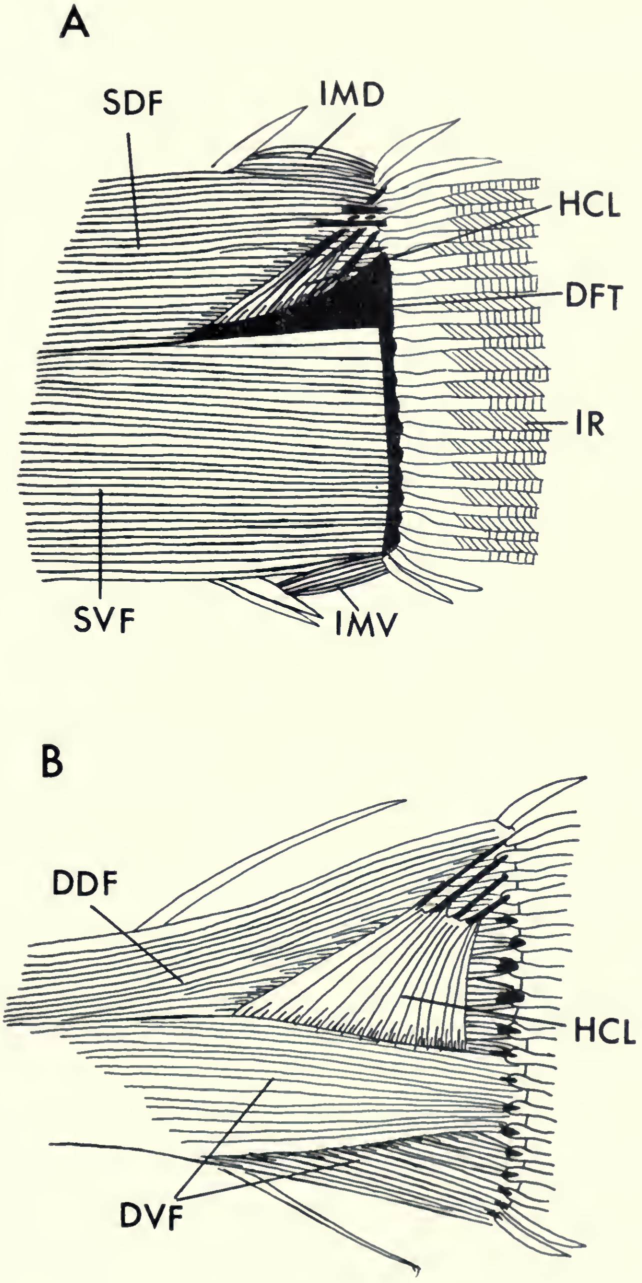
FIG. 40. A, Superficial caudal musculature of *Polycentropsis abbreviata*. B, Deep caudal musculature after removal of superficial flexors. DDF, deep dorsal flexor muscle; DFT, deltoid flexor tendon; DVF, deep ventral flexor muscle; HCL, hypochordal longitudinal muscle; IMD, dorsal carinalis muscle; IMV, ventral carinalis muscle; IR, interradial muscles; SDF, superficial dorsal flexor muscle; SVF, superficial ventral flexor muscle.


A
SDF
IMD
HCL
DFT
IR
SVF
IMV
B
DDF
HCL
DVF

can be flexed when closed as well as when open, indicating that various muscle groups can act either simultaneously or independently.

15. MUSCLES OF THE PECTORAL FINS

The pectoral musculature conforms to that of generalized percoids as described by Grenholm (1923).

The *superficial abductor muscle* is composed of two heads (Fig. 41: ABS). The fleshy origin of the outer head is on the inner surface of the cleithrum. The tendinous insertion is on the more ventral fin rays. The second, inner head originates more ventrally to the origin of the outer head. It inserts by an aponeurosis to the more dorsal fin rays.

Deep to the superficial abductor muscles are the arrector ventralis and the abductor profundus muscles.

The spindle-shaped *arrector ventralis muscle* originates from the medial surface of the cleithrum and inserts tendinously on the first fin ray (Fig. 41: AR).

The *abductor profundus muscle* originates from the coracoid, scapula, and cleithrum and is inserted by very short tendons to all fin rays (Fig. 41: ABP).

On the medial aspect of the pectoral girdle are the adductors.

The trapezoid *adductor superficialis muscle* takes its fleshy origin from the medial surface of the cleithrum, dorsal to the origins of the abductors, and inserts to all fin rays by long, slender tendons (Fig. 41: AS).

The rectangular *adductor profundus muscle* is deep and ventral to the adductor superficialis muscle. It inserts on all fin rays by tendons, proximal to the insertion of the superficial adductor (Fig. 41: AP).

The adductors cover the following two muscles:

The triangular *arrector dorsalis muscle* has a broad origin on the medial surface of the cleithrum and converges to insert on several dorsal rays (Fig. 41: AR).

The relatively large and rectangular *arrector radialis muscle* originates from the radials and coracoid and inserts on several more ventral fin rays.

All nandids make extensive use of the pectoral fins during their stealthy approach toward their prey. During forward movement a wave travels across the pectoral fin from top to bottom. The fin, at first, is held against the body. The more dorsal fin rays are erected

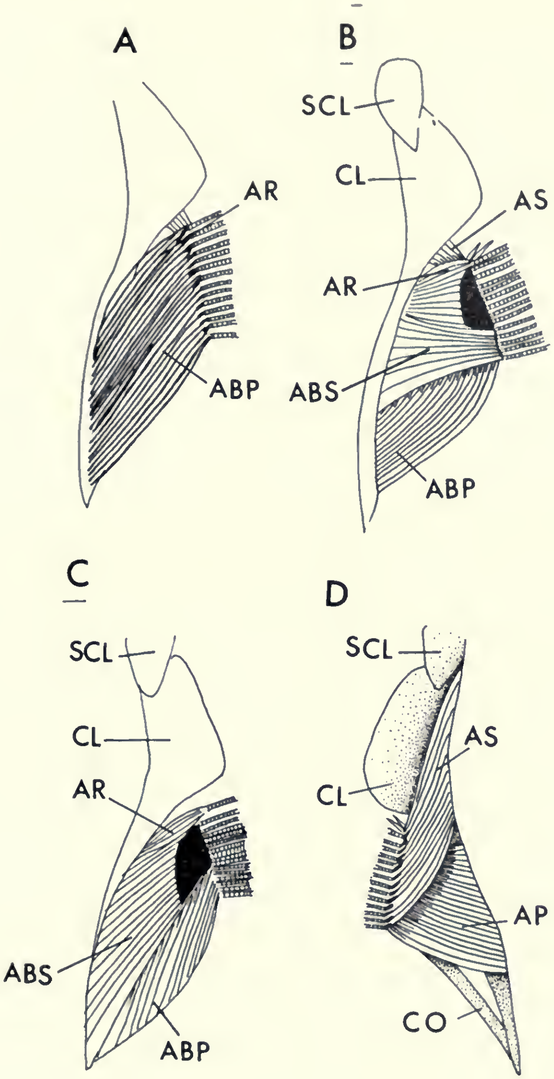


FIG. 41. A, lateral aspect of superficial pectoral musculature of *Nandus nebulosus*; B, lateral aspect of pectoral musculature after removal of abductor superficialis muscle; C, lateral aspect after removal of the entire abductor superficialis muscle; D, medial aspect of pectoral musculature. ABP, abductor profundus muscle; ABS, abductor superficialis muscle; AP, adductor profundus muscle; AR, arrector dorsalis muscle; AS, adductor superficialis muscle; CL, cleithrum; CO, coracoid; SCL, supracleithrum.

first through contraction of the arrector ventralis muscle, which spreads the fin somewhat, drawing the fin forward and slightly ventral. This is followed by similar movements of the following and successive fin rays by action of the abductor superficialis muscles. The degree of phase difference between the dorsal and ventral fin rays is such that the forward-moving fin exerts little pressure on the water. However, during backward movement of the fin the phase difference between successive fin rays is negligible and the fin moves as a rigid flat surface, exerting considerable pressure backward on the water by co-ordinated contraction of the adductor superficials, adductor profundus, and arrector dorsalis muscles.

During backward locomotion of the fish, the phase difference in the movement of successive fin rays is decreased when the fin is turned forward against the head. The fin is moved backward with a great phase difference abolishing the pressure exerted on the water. The arrector radialis muscle may play an important role in the reversed wave, i.e., from bottom to top, during backward locomotion of the fish (Harris, 1938).

The pectoral may beat simultaneously or alternately with varying amplitudes depending on environmental conditions.

16. MUSCLES OF THE PELVIC GIRDLE

The organization of pelvic musculature of the Nandidae agrees generally with that of generalized percoids as described by Grenholm (1923). The basipterygii and the muscles attaching to it are more or less enclosed in the rectus abdominus part of the body musculature. Ventrally, three muscles are attached to each half of the pelvic girdle: the superficial and deep abductors and the arrector ventralis muscles.

The *abductor profundus muscle* is covered ventrally by the abductor superficialis muscle (Fig. 42: ABS). Its origin from the ventral surface of the basipterygium is more medial to that of the superficial abductor. The insertion is by separate tendons to all soft fin rays.

The spindle-shaped *arrector ventralis muscle* originates from the ventrolateral edge of the basipterygium and inserts by means of a strong tendon on the ventral side of the basis of the pelvic spine (Fig. 42: ARV).

The large, well-developed *arrector dorsalis muscle* originates from the lateral surface of the basipterygium, immediately dorsal to the arrector ventralis muscle (Fig. 42: ARD). The tendinous insertion is on the lateral surface of the basis of the pelvic spine.

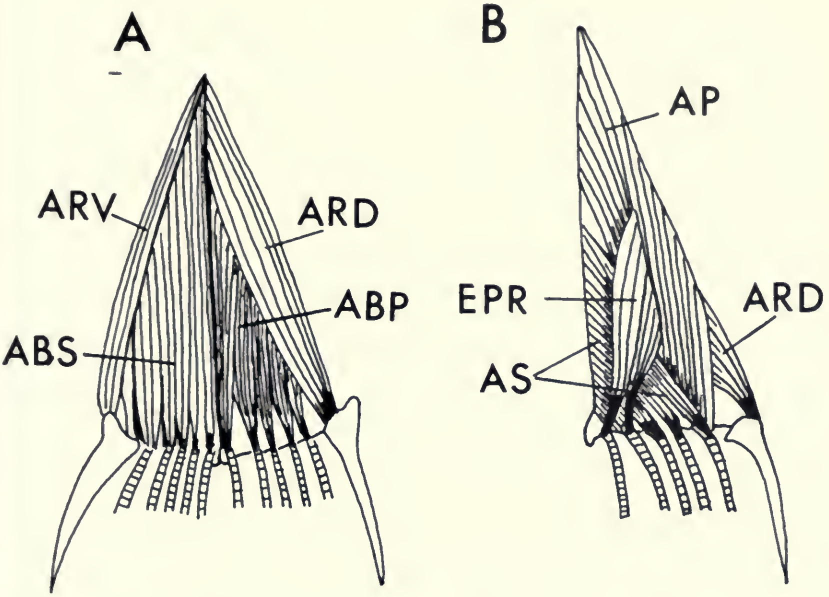


FIG. 42. A, ventral aspect of pelvic musculature of *Nandus nebulosus*. Superficial layer has been removed from left side. B, dorsal aspect of pelvic musculature of right half. ABP, abductor profundus muscle; ABS, abductor superficialis muscle; AP, adductor profundus muscle; ARD, arrector dorsalis muscle; ARV, arrector ventralis muscle; AS, adductor superficialis muscle; EPR, extensor proprius muscle.

Three muscles are attached to the dorsal surface of each basipterygium: the superficial and deep adductors and the extensor proprius muscle.

The triangular *extensor proprius muscle* is the most dorsal muscle, originating from the laterodorsal wall of the basipterygium. The fibers run posteromedially to converge on two to three tendons that insert on two to three median soft rays (Fig. 42: EPR).

The *adductor superficialis muscle* lies immediately ventral to the extensor proprius muscle. The fleshy origin is from the medial edge of the dorsal aspect of the basipterygium. The fibers run posterolaterally from their origin to insert by separate tendons on the dorsal surfaces of the bases of all soft fin rays (Fig. 42: AS).

The *adductor profundus muscle* is the largest and most ventral muscle on the dorsal aspect of the basipterygium (Fig. 42: AP). It originates virtually from the entire dorsal aspect of the basipterygium, excluding the surface occupied by the two other muscles. The fibers converge on the separate tendons that insert on the bases of all the soft rays.

The pelvic fins do not contribute to active locomotion. The pelvic fins become effective and functional only when the fish is already moving. The nandids seem to resemble generalized percoids in respect to pelvic function as described by Harris (1938). The nandids normally swim with the pelvic fins closed against the body or extended with the fin rays in a plane parallel to the long axis of the fish. *Monocirrhus* often backs up with the fins closed. Closure of the fins against the body surface is the result of contraction of the adductor superficialis muscles. Spreading the pelvic fin is effected by contraction of the arrector dorsalis and ventralis muscles, which pull the spine ventrally and laterally. The erector of the spine will pull the pelvic membrane and connected fin rays open. The abductor superficialis and profundus muscles will draw the soft fin rays ventrally. This pressure downward against the water will lift the fish up. The extensor proprius muscle plays a major role in raising the medial border of the fin (Harris, 1938). The extensor proprius and adductor profundus muscles pull the fin dorsally from its neutral position. This will result in a downward movement of the fish. The adductor system is better developed than the abductor apparatus in nandids, indicating that the production of a downward force is an important function.

Ligaments and Arthrology

A thorough study of the joints and ligaments is extremely important in functional analysis. Joints and ligaments determine the direction, degree, and speed of motions between two or more bony elements. The presence of ligaments often causes a long chain of motions in a series. Couplings between functional units can be traced and understood only by a thorough descriptive knowledge of the ligaments and joints. The following description will serve for the background to the chapter on functional analysis. The ligaments have been grouped topographically, rather than functionally. This grouping is for the purpose of clarity. In most cases this grouping reflects function, except for the ligaments associated with the jaw apparatus. The functions are discussed in the chapter on functional analysis.

1. LIGAMENTS

1. Intrinsic ligaments of the jaw apparatus

a. *Ligamentum primordiale* (ligamentum maxillo-mandibulare posterius of van Dobben (1937)); the articular-maxillary ligament of Alexander (1967) is a distinct tract of collagen fibers that runs from the lateral face of the head of the maxilla to the lateral face of the mandible near the quadratomandibular joint (Fig. 29: PRL) in *Nandus*. The ligamentum primordiale is absent in other investigated nandids. The ligamentum primordiale should not be confused with the insertion tendon of the adductor mandibulae muscles. The entire tract is well differentiated in *Nandus* and the dorsal attachment to the lateral ridge of the head of the maxilla is rather extensive.

b. *Ligamentum maxillomandibulare mediale* (ligamentum maxillomandibulare anterius of van Dobben (1937)) is a strong tract of collagen fibers connecting the median face of the ventral end of the maxilla to the ascending process of the dentary (Figs. 43–45: MMM). This ligament is well differentiated in all nandids.

c. *Ligamentum maxillomandibulare anterius* (Kayser, 1962) is a complex tract of collagen fibers between the ventral ends of the pre-

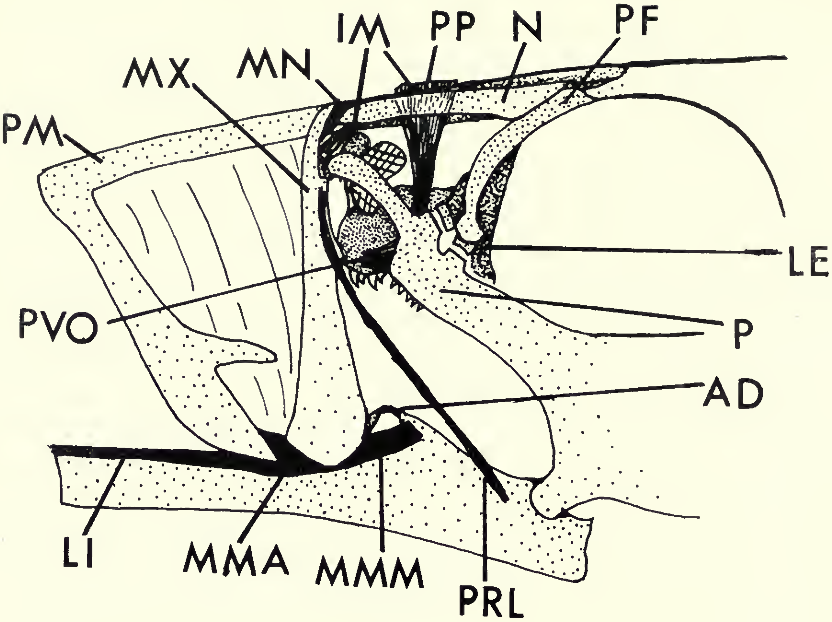


FIG. 43. Lateral aspect of deep dissection of preorbital region of *Nandus nebulosus* to exhibit joints and ligaments. AD, angulodental ligaments; IM, intermaxillary ligament; LE, lateral ethmoid; LI, lip; MMA, anterior maxillomandibular ligament; MMM, medial maxillomandibular ligament; MN, maxillonasal ligament; MX, maxillary; N, nasal; P, palatine; PF, prefrontal; PM, premaxilla; PP, palatopalatine ligament; PRL, primordial ligament; PVO, palatovomerine ligament.

maxilla and maxilla and the dorsolateral margin of the dentary (Figs. 43–45: MMA). The attachments to the dentary are most extensive in *Nandus* and *Polycentrus* in which it occupies the entire length of the dentary. The tract splits into two directions posteriorly. One branch extends between the dentary and ventral end of the premaxilla, while the second branch connects the dentary with the ventral end of the maxilla. This ligament contributes to the corners of the lips.

d. *Ligamentum angulodentale* occurs in all nandids as a very strong tract bridging the gap between the ascending processes of the dentary and angular (Figs. 43–45: AD). This ligament is common in percoids, but it has not been described in previous literature.

e. *Ligamentum premaxillomaxillare* may represent a subdivision of the ligamentum maxillomandibulare anterius. The distinct connective tissue tract runs between the ventral ends of the premaxilla and maxilla (Fig. 44: MMA). Interconnections between this ligament and the ligamentum maxillomandibulare anterius are common in nandids.

f. *Ligamentum intermaxillare* is not well differentiated in nandids. No distinct condensation of connective tissue fibers between the dorsal tips of the maxillae has been found. However, there is a somewhat thickened dermis between the heads of the maxillae.

2. Ligaments between suspensory apparatus and jaws

a. *Ligamentum palatomaxillare posterior* is present in all nandids, except *Nandus* (Figs. 44, 45: PMX). Two distinct branches are differentiated. The first is long and narrow, extending between the lateral surface of the center of the body of the palatine and the posterior surface of the head of the maxillae. The length of the ligament is proportional to the length of the ascending processes of the premaxillae. The second subdivision of the palatomaxillare originates more dorsally on the lateral surface of the body of the palatine and runs to the cranial condyle of the maxilla.

b. *Ligamentum palatomaxillare anterior* (ligamentum palatomaxillare of Kayser (1962)) is a short fan-shaped ligament connecting the dorsal head of the palatine to the medial surface of the head of the maxilla. This connection is present in all nandids.

c. *Ligamentum palatopremaxillare* is absent in nandids.

d. *Ligamentum quadratomandibularis laterale* forms together with the

e. *Ligamentum quadratomandibularis mediale,* a system of collateral ligaments around the quadratomandibular joint. Both ligaments are short, but distinct and strong tracts, reinforcing and stabilizing the joint. The lateral ligament runs from the lateral surface of the lower half of the condyle of the quadrate to the slight elevation on the lateral surface of the angular just ventral and posterior to the fossa of the quadratomandibular joint. The medial ligament is slightly broader. It runs between the medial surface of the quadrate to the medial surface of the retroarticular.

No distinct ligaments are found between the maxilla and the ethmoid, and the lateral ethmoid and lachrymal.

3. Ligaments between neurocranium and jaws

Ligamentum maxillonasale is a strong, short tract of collagenous fibers between the posterior margin of the dorsal part of the head of the maxilla and the anterolateral margin of the nasal bones.

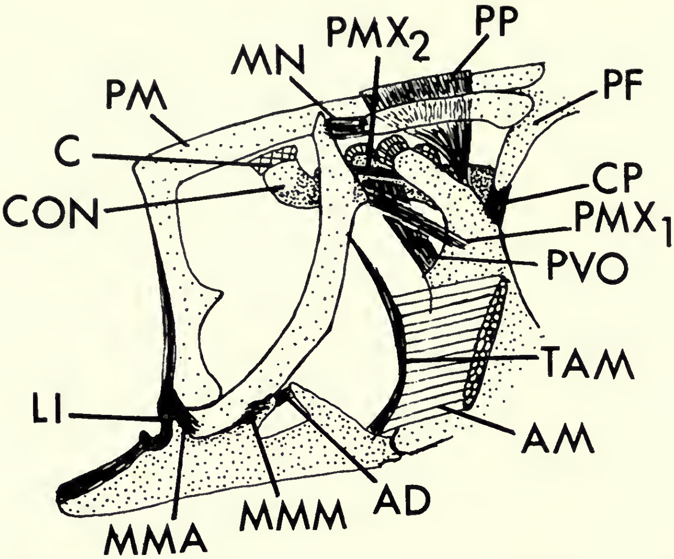


FIG. 44. Lateral aspect of deep dissection of preorbital region of *Polycentrus schomburgkii* to exhibit joints and ligaments. AD, angulodental ligament; AM, adductor mandibulae muscle; C, cartilaginous meniscus; CON, condylar process of maxilla; CP, craniopalatine ligament; LI, lip; MMA, anterior maxillomandibular ligament covered by premaxillomaxillary ligament; MMM, medial maxillomandibular ligament; MN, maxillonasal ligament; PF, prefrontal; PM, premaxillary; PMX$_1$, first posterior palatomaxillary ligament; PMX$_2$, second posterior palatomaxillary ligament; PP, palatopalatine ligament; PVO, palatoprevomerine ligament; TAM, tendon of adductor mandibulae muscle.

This ligament is very well developed in all nandids. It attaches the head of the maxilla firmly to the nasal (Figs. 43–45: MN).

4. Ligaments between suspensory apparatus and neurocranium

a. *Ligamentum craniopalatini* (Figs. 44, 45: CP) is a broad, thick tract of collagenous fibers descending from the ventral surface of the lateral ethmoid. The ligament attaches to the dorsal margin of the posterior portion of the body of the palatine. This strong ligament is the only anchor at the anterodorsal corner of the suspensory apparatus in all nandids, except *Nandus*. *Nandus* lacks the craniopalatine ligament. Instead, the suspensory apparatus articulates with two joints to the prefrontal-lateral ethmoid complex (Fig. 43).

b. *Ligamentum palatoprevomer* is a strong band of collagenous fibers running between the anterior border of the body of the palatine and lateral surface of the head of the prevomer. This ligament is present in all nandids (Figs. 43, 45: PVO). It is best developed in *Nandus*.

5. Ligaments between opercular apparatus and the jaws

The *ligamentum mandibulo-interoperculare* is the only ligament between these two units. The ligament is relatively long and distinct (Figs. 29, 32, 33: LIM). It extends between the anterior margin of the interopercular and the posterolateral margin of the retroarticular. In *Nandus* and *Afronandus* the ligament is horizontal (Fig. 29), while in all other genera the ligament is subvertical.

6. Intrinsic ligaments of the opercular apparatus

Only one ligament is differentiated, the *interoperculo-opercular ligament,* between the anteroventral margin of the opercular and the posterodorsal corner of the interopercular. This vertical ligament (Figs. 29, 33: IOPL; Fig. 32: IOL) is found in all nandids.

Undifferentiated connective tissue is found between the opercular, subopercular, and preopercular bones.

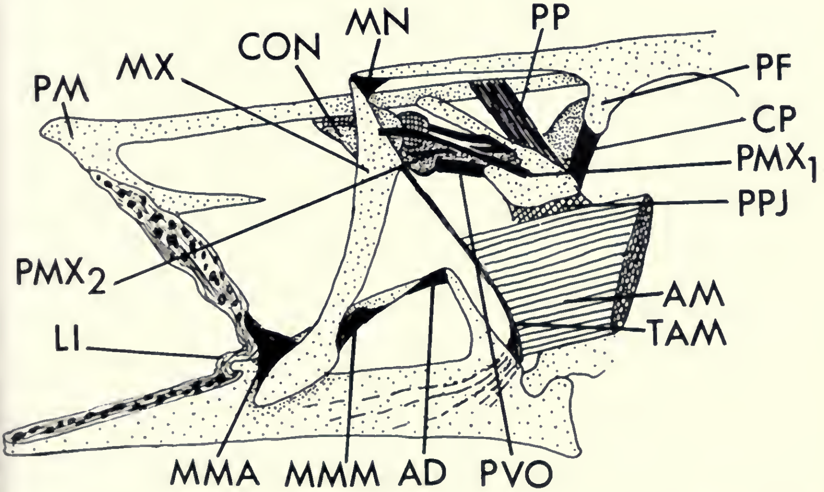


FIG. 45. Lateral aspect of deep dissection of preorbital region of *Monocirrhus polyacanthus* to exhibit joints and ligaments. AD, angulodental ligament; AM, adductor mandibulae muscles; CON, condylar process and meniscus; CP, craniopalatine ligament; LI, lip; MMA, anterior maxillomandibular ligament; MMM, medial maxillomandibular ligament; MN, maxillonasal ligament; MX, maxilla; PF, prefrontal; PM, premaxilla; PMX_1, first posterior palatomaxillary ligament; PMX_2, second posterior palatomaxillary ligament; PP, palatopalatine ligament; PPJ, palatopterygoid joint; PVO, palatoprevomerine ligament; TAM, tendon of adductor mandibulae muscle.

7. Ligaments between opercular and hyoid apparatus

In *Nandus* two ligaments extend between the medial surface of the interopercular and the lateral surface of the epihyal (Fig. 35: IHL). These ligaments are the *interoperculohyoid ligaments.* In all other nandids only one strong and distinct interoperculohyoid ligament is found (Figs. 36–38).

8. Intrinsic ligaments of the suspensory apparatus

Ligamentum palatopalatini (interpalatine ligament) is extremely well developed in all nandids. The ligament is a continuous tract between the palatines of either side (Figs. 43–45: PP). The ligament is attached to the dorsal margin of the body of the palatine just below the origin of the maxillary process. The attachment to the palatine represents the narrowest portion of the ligament. Dorsally, the ligament expands and runs over the ascending processes of the premaxillae.

9. Ligaments between hyoid apparatus and branchial basket

Only one pair of ligaments connects these two units. The *ligamentum hypohyalobasibranchiale* extends between the dorsomedial margin of the posteromedial corner of the dorsal hypohyal and the anterolateral surface of the first basibranchial. The ligament is narrow and elongate.

10. Intrinsic ligaments of the hyoid apparatus

a. *Ligamentum interhyoideus* is a distinct tract of connective tissue extending transversely between the posteromedial corners of the ceratohyals. This ligament passes ventral to the ligamentum hypohyalobasibranchiale and runs in a horizontal plane.

b. *Ligamentum urohyalohypohyale* is present in all acanthopterygians. It is a short, stout tract between the anterior process of the urohyal and the posteroventral surface of the hypohyal (Figs. 37, 38: UHL). This ligamentous connection is very strong.

11. Intrinsic ligaments of the branchial apparatus

a. *Ligamentum hypobranchialobasibranchiale*$_1$ and $_2$ are two ligaments running, respectively, from the dorsal surface of the first basibranchial to the dorsal surface of the medial corner of the hypobranchial and from the ventral surface of the first hypobranchial to the dorsal surface of the second basibranchial.

b. *Ligamentum basibranchialoceratobranchiale* connects the anterior tip of the fifth ceratobranchial to the posterior margin of the last basibranchial.

c. *Ligamentum interbranchiale* consists of three pairs of elongate, narrow tracts that extend between the ventral ends of the ceratobranchials between the four anterior successive branchial arches.

II. ARTICULATIONS

Only mobile junctions between bony elements are discussed. Syndesmoses are omitted. The joints are discussed descriptively. The various motions will be analyzed in detail under "Motion Analysis." Most of the joints have been studied grossly, but some are based on histological observations. The joints are treated topographically in relation to the proposed functional units.

1. Joints between neurocranium and suspensory apparatus

Two articulations are usually present between these units.

a. The *craniohyomandibular joint* is synovial. Two articular heads of the hyomandibular are differentiated, but the two heads are continuous. The two heads are lodged in a continuous longitudinal groove on the ventral surface of the sphenotic and pterotic (Figs. 9, 10). The groove is lined with articular cartilage which, in turn, forms a concavity to receive the cartilage on the heads of the hyomandibular. The capsule of the joint is well developed. The principal movement of the hyomandibular is mediolateral. Protraction and retraction are inhibited by the strong bony walls bordering, respectively, the anterior and posterior margins of the articular fossa. The longitudinal axis of the joint parallels the lateral border of the pterotic and sphenotic (Figs. 9, 10) and runs at an angle of approximately 15 degrees with the longitudinal axis of the cranial base.

b. The *palatocranial joint* varies in the different nandid genera. The articulation is non-synovial.

In *Nandus* the palatine articulates with two articular surfaces on the prefrontal lateral ethmoid complex. The articular processes are differentiated on the dorsomedial margins of the palatine (Fig. 43). The anterior articular process is located at the base of the maxillary process of the palatine. The articular plane runs parallel with the ventral margin of the palatine. The posterior articular process of the palatine is just ventral to the lateral wing of the prefrontal. Its articular plane parallels the ventral border of the palatine. Distinct articular menisci are between both articulations.

In all other nandids the palatine does not articulate with the neurocranium. The palatine is connected to the prefrontal lateral ethmoid complex by a strong and prominent ligament (Figs. 44, 45: CP).

2. Joints between suspensory apparatus and jaws

a. The *palatomaxillary joint* is nonsynovial. The tip of the maxillary process of the palatine is rather firmly attached by short ligaments to the lateral surface of the head of the maxilla. This articulation is present in all nandids. No subpalatine meniscus has been found.

b. The *quadratomandibular joint* is synovial and can be regarded as a modified saddle joint. The articular head of the quadrate is subdivided into two components, a medial and a lateral articular head. The articular surface of the medial head is directed posteriorly. The lateral head has its articular surface facing anteriorly. The fossa of the quadratomandibular joint is located in the angular. The fossa has two distinct articular surfaces, which accommodate the two articular heads of the quadrate. The lateral horizontal articular surface lodges the anteriorly-directed lateral head of the quadrate. The medial vertical articular surface corresponds with the posteriorly-directed medial head of the quadrate (Fig. 59). The angle between the articular surfaces of the angular is less acute than the angle between the two articular surfaces of the quadrate. Consequently, only one set of articular surfaces is in close contact at any one time.

3. Joints between suspensory apparatus and opercular apparatus

The *operculohyomandibular joint* between the opercular and the opercular process of the hyomandibular is synovial. The opercular process of the hyomandibular is differentiated into a rounded articular head which is lodged in a rounded socket on the medial aspect of the opercular. This ball and socket joint provides great mobility along three axes. The opercular bone can rotate along a transverse axis and move mediolaterally.

4. Intrinsic joints of the suspensory apparatus

Although cartilage is often present between the bony elements of the suspensory apparatus, mobile joint-like connections have been recorded in only a few teleosts, e.g., in *Epibulus* (Delsman, 1925), *Callionymus* (Kayer, 1962), and *Bunocephalus* (Shafland, 1968). *Monocirrhus* is unique among nandids in having a distinct and large cartilage between the palatine and pterygoids (Figs. 16, 33, 45). The palatine can move independently of the rest of the suspensory apparatus. The cartilaginous plate between palatine and pterygoids is highly flexible. The palatine is connected to the head of the maxilla and to the prefrontal by means of ligaments. No articulations are found between palatine and neurocranium. The mobile palatopterygoid joint is a synchondrosis in *Monocirrhus*. The other nandid genera lack this joint.

5. Joints between the jaw apparatus and neurocranium

a. The *premaxilloneurocranial joint* is found between the ascending process of the premaxillae and the rostral fossa on the dorsal aspect of the neurocranium. The ascending process can slide in an anteroposterior direction over a considerable distance. No special cartilages are found lining the rostral fossa. The joint is not synovial. Some cartilage is found in the anterior portion of the rostral fossa and on the posterior tips of the ascending processes. The rostral fossa is covered by connective tissue membranes and integument. The ascending processes are kept in the rostral fossa by the palatopalatine ligament (Figs. 43–45: PP).

b. The *maxilloprevomerine joint* is found between the posterior median part of the maxillary head and the prevomer. The posterior median part of the maxillary head is differentiated into a cranial condyle, which is provided with a submaxillary meniscus to articulate with the anterolateral surface of the prevomer (Figs. 43–45).

6. Intrinsic joints of the jaw apparatus

The *maxillopremaxillary joint* in nandids is different from that described for the generalized acanthopterygian by Alexander (1967). Nandids lack the articular process of the premaxilla. The anterior median part of the head of the maxilla is differentiated into a well-developed premaxillary condyle with a distinct meniscus (Figs. 43–45). The ventral surface of the ascending process of the premaxilla glides on the premaxillary condyle. The premaxillary condyles of either side form a groove-like structure accommodating the ascending process of the premaxillae. The maxillopremaxillary joint is the only one intrinsic to the jaw apparatus.

7. Intrinsic joints of the branchial apparatus

The joints between the various bony elements of the branchial apparatus are essentially similar. The description here applies to the junction between the ceratobranchial and epibranchial bones.

However, the junctions between hypobranchial and basibranchial exhibit the same features. The only differences found are in the amount of cartilage.

The whole epiphysis of the ceratobranchial is made of hyaline cartilage (Fig. 66). There is no typical articular surface such as in the joints of tetrapods. No joint cavity exists between the articulating bones. Movement is allowed by a layer of loose connective tissue between the cartilaginous epiphyses of the two bones. The large cartilaginous epiphysis minimizes any sudden shock to the bony system, and at the same time allows the transmission of muscular forces from one bone to another (Haines, 1934). The massive cartilaginous masses will result in a high degree of elasticity in the intrinsic joints of the branchial apparatus.

8. Joints between branchial apparatus and neurocranium

The branchial apparatus is suspended from the neurocranium by the first pharyngobranchial. The junction between the first pharyngobranchial and the prootic is ligamentous. This junction is mobile, yet firm. No articular cartilage has been found. The junction between first pharyngobranchial and first epibranchial is as described in section 7 above, for the junction between ceratobranchial and epibranchial.

9. Joints between hyoid apparatus and suspensory apparatus

The rod-like interhyal has a massive cartilaginous epiphysis, which is attached to the cartilaginous head of the symplectic process of the hyomandibular. A thin layer of loose connective tissue separates the adjoining cartilages. The junction between interhyal and epihyal is similar to that described for the junction between ceratobranchial and epibranchial.

Osteological Definition of the Nandidae

No single osteological feature separates the Nandidae from other percoid families, such as the Pristolepidae and Lobotidae.

However, all the nandids share a common combination of morphological features that distinguishes the Nandidae from other percoid families. The combination of morphological features may reflect an adaptive pattern for the highly specialized predaceous feeding habits. It is virtually impossible to select only those taxonomic features that are not involved in the shared adaptive pattern. The entire skull is involved in the feeding mechanism. The locomotory apparatus, including the pectoral and pelvic osteology and myology, the median fins, and the caudal fin are closely correlated with similar feeding habits. All nandids float in the water mimicking dead leaves and capturing their prey by extremely fast motions. The digestive tract, the pleuroperitoneal cavity, and other viscera are undoubtedly correlated with the feeding habits. Therefore, one cannot avoid using morphological characters that are specifically adaptive to a shared ecology in the characterization of the Nandidae. It is impossible to prove whether the characters shared by all nandids are the result of common ancestry or the product of a common selection pressure on a phylogenetically diverse assemblage of fishes. However, the use of multiple characters and a careful analysis of the functional units on a comparative basis will bring us closer to an understanding of the evolutionary pathways than any other approach. Some characters form a chain, which represents a coupling, in either opening or closing the jaws. The structures involved in a coupling are highly interdependent in performing one function (Liem, 1967b). A change in one element of the coupling will elicit changes in the other elements of the coupling if the original function is to be preserved (Liem, 1967b). These changes within a coupling may involve characters of very different topography and structure (e.g., muscles, ligaments, bones, blood vessels, and sense organs). These couplings can be recognized only by functional analysis. And, regardless of topography or structural constitution, elements of one coupling can be considered as only one taxonomic character in phylogenetic, phenetic, or numerical taxonomy. In this chapter an osteological characterization is given for the purpose of a taxonomic definition of the family. The meaning of the characters and the phylogenetic implications are made after the chapter on functional analysis.

The Nandidae share all characters enumerated for the Percoidei by Regan (1913, p. 113). The following combination of osteological features occur in all Nandidae and may be regarded as a characteristic nandid pattern, although no single osteological feature distinguishes the family from other percoids.

The neurocranium possesses a prominent rostral fossa involving the frontal and ethmoid bones. The rostral fossa reaches posteriorly to the supraoccipital bone. Three longitudinal crests are present on the dorsal aspect of the neurocranium. Two parietal crests are on the epiotics, parietals, and posterior halves of the frontals. The third median supraoccipital crest is restricted to the supraoccipital bone. Beyond the supraoccipital the crest either disappears or splits to continue along each lateral rim of the rostral fossa. The frontals are large bones, covering the anterior two-thirds of the cerebral skull. The circumorbitals do not form a subocular shelf. The hyomandibular possesses a knob-like, rounded anterior head and an elongate posterior head with a straight dorsal margin. The anterior margin of the body of the hyomandibular is differentiated into a ventrally-directed spine that meets with a dorsally-directed projection of the metapterygoid. The large metapterygoid is joined to the symplectic process of the hyomandibular. The preopercular has a very short horizontal limb. The triangular opercular is directly connected to the interopercular by means of the interoperculo-opercular ligament. The subopercular is not interposed between the opercular and interopercular.

The mandible is very long. Its length equals the total length of the neurocranium. The shortest mandible measured is three-quarters the length of the neurocranium. The dentary forms the anterior half of the mandible, while the posterior half is occupied by the angular. The premaxillae possesses exceptionally long ascending processes. Articular processes of the premaxillae are absent. The large and elongate maxillae have well-differentiated cranial and premaxillary condyles. The distal extremity of the alveolar process of the premaxilla is connected to the outer face of the ventral corner of the maxilla by the premaxillomaxillary ligament. Two basibranchials are present. The first epibranchial is distinctly forked dorsally. The caudal skeleton has five hypurals (using Nybelin's (1963) system of counting), which are subequal in width and splayed out like the spokes of a fan. One epural is present, and the last hemal arch is in contact with the urostyle. The penultimate (second pre-ural) possesses a complete secondary neural arch, except in *Afronandus*. There are 23 vertebrae of which the precaudals have parapophyses from the seventh or eighth.

Some of the characters enumerated for the Nandidae by Regan (1913, p. 129) are not generally applicable to the family. The rostral fossa is certainly not formed by the bifurcation of the occipital crest. The connection between the premaxilla and maxilla is not an articulation, but a simple ligamentous junction. Teeth on prevomer and palatines occur in only one genus, i.e., *Nandus*, while all the other nandids lack prevomerine and palatal teeth consistently.

Intergeneric Differences and Similarities

Although the Nandidae represent a rather uniform assemblage, the genera are easily distinguished on a morphological basis.

Nandus possesses a number of characteristic features, which do not occur in other nandid genera. It possesses broad nasals, while all other genera have slender, rod-like nasals. Patches of villiform teeth are found on the ectopterygoid, the dorsal surface of the third hypobranchials, the palatine, the prevomer, and the parasphenoid. The joint between the palatine and prefrontal is composed of two pairs of articular surfaces. The adductor mandibulae muscles are differentiated into three distinct heads. *Nandus* lacks the posterior palatomaxillary and craniopalatine ligaments, which are present in other nandids. *Nandus* is unique among nandids in having a well-differentiated primordial ligament in the jaw apparatus. The interoperculohyoid ligament is composed of two distinct parts.

Nandus and *Afronandus* share several features which do not occur in the other three genera. Large elongate fontanelles are found in the rostral fossa in the anteromedial corners of the frontals (Figs. 1, 2). Both genera have a straight cranial base, elongate and relatively large ectopterygoids, and 13 precaudal and 10 caudal vertebrae. The mandibulo-interopercular ligament is horizontally placed.

Afronandus can be distinguished by the small nasals, the small parietal crests restricted to the epiotic and posterior half of the parietal (Figs. 2, 5), and the absence of a secondary neural arch on the second pre-ural centrum (Fig. 27).

Polycentropsis and *Monocirrhus* have many distinguishing features in common. The quadrate is vertical, and the metapterygoid is joined to both the entopterygoid and ectopterygoid (Figs. 15, 16). The ascending process of the premaxillary and the basihyal are much longer than in the other three genera. The entopterygoid is very small. The intramandibularis portion of the adductor mandibulae muscles is vestigial, but the pharyngohyoideus muscle attains its greatest development in these two genera. The origin of the levator operculi muscle is tendinous and restricted to the posterolateral corner of the pterotic. The protractor hyoideus muscle is much more elongate than in the other three genera.

Polycentropsis possesses two distinguishing characters: the circumorbitals are interrupted and there is a distinct ascending process of the prevomer suturally united with a process of the prefrontal-lateral ethmoid complex (Figs. 7, 20).

Monocirrhus is unique in having a mobile synchondrosis between the palatine and the pterygoids (Fig. 16) and non-serrated preopercular (Fig. 21).

In *Polycentrus* the serration of the preopercular is restricted to the ventral border of the horizontal limb (Fig. 19). The five genera can easily be separated on the pattern of serration of the preopercular (Figs. 17–21). No other feature singles out *Polycentrus*. However, *Polycentrus* has a characteristic complex of morphological features: The opercular has two to seven small spines (Fig. 19), the interopercular is serrate, the adductor mandibulae muscle is differentiated into two well-developed heads, the lachrymal is serrate (Fig. 19), and the entopterygoid is joined with both the ectopterygoid and quadrate (Fig. 14).

Motion Analysis

1. FEEDING HABITS IN THE LABORATORY

Live specimens of *Polycentrus schomburgkii, Nandus nebulosus,* and *Monocirrhus polyacanthus* have been observed in aquaria under laboratory conditions. The aquaria were furnished with gravel bottoms and plants restricted to one corner.

Nandus nebulosus remained extremely shy. This species feeds on large earth worms, *Tubifex,* and occasionally takes small guppies. It picks up worms from the bottom. When catching small guppies, *N. nebulosus* drifts very slowly toward its prey, using minimal movements of its fins. It approaches the prey frontally, with the head slightly down exposing the light interobital line on the head. When close enough, this predator protrudes its jaws (too rapidly to be followed by the eye) without jerking its body (Fig. 47). Only five attempts of this kind have been observed. Three were successful, while in two cases the prey escaped without any further pursuit by the predator. No motion pictures were made of this species. Its shyness prevented any further attempt at objective recording of the motions of the jaws. In nature *N. nebulosus* feeds on aquatic insect larvae and small fish (Inger and Chin, 1962, p. 165).

Polycentrus schomburgkii seems less shy and feeds on *Tubifex,* earth worms, chopped beef heart, and small fishes (guppies, *Acanthophthalmus kuhlii,* and small *Clarias*). It feeds readily on the surface of the water, at midwater, and from the bottom. Its approach toward live fishes is rather similar to that of *Nandus nebulosus* (Barlow, 1967a). It drifts slowly toward the prey with minimal movements of the body. Capture is accomplished by exceedingly rapid movement of the jaws (Fig. 48). In 45 attempts, 35 were successful at the first approach. *Polycentrus* pursues its prey frequently after failing to catch it.

Monocirrhus polyacanthus feeds exclusively on live or disabled fishes. I have never been able to feed *Monocirrhus* any other kind of food than live fish. It refuses freshly-killed fish, live worms, or chopped beef heart. Several specimens died of starvation in absence of live fish as prey. This species drifts slowly and imperceptibly toward the unsuspecting prey. The mode of swimming is with the head at a downward angle, exposing the cream-colored interorbital line of the head in a frontal approach (Barlow, 1967a). Then, in one motion, too fast for the eye to follow, the prey is virtually inhaled. Swallowing of large prey can last for an hour. This species was fed with guppies, albino *Clarias* sp., and *Acanthophthalmus kuhlii*. The spines of the pelvic fins of *Clarias* were removed.

No original observations have been made on the feeding behavior of *Afronandus sheljuzhoi* and *Polycentropsis abbreviata*. *Afronandus* was fed *Daphnia* by Scheel (1964), who remarked that in nature this species is highly predaceous. The African leaf-fish, *Polycentropsis abbreviata,* is said to resemble the South American leaf-fish in respect to feeding behavior.

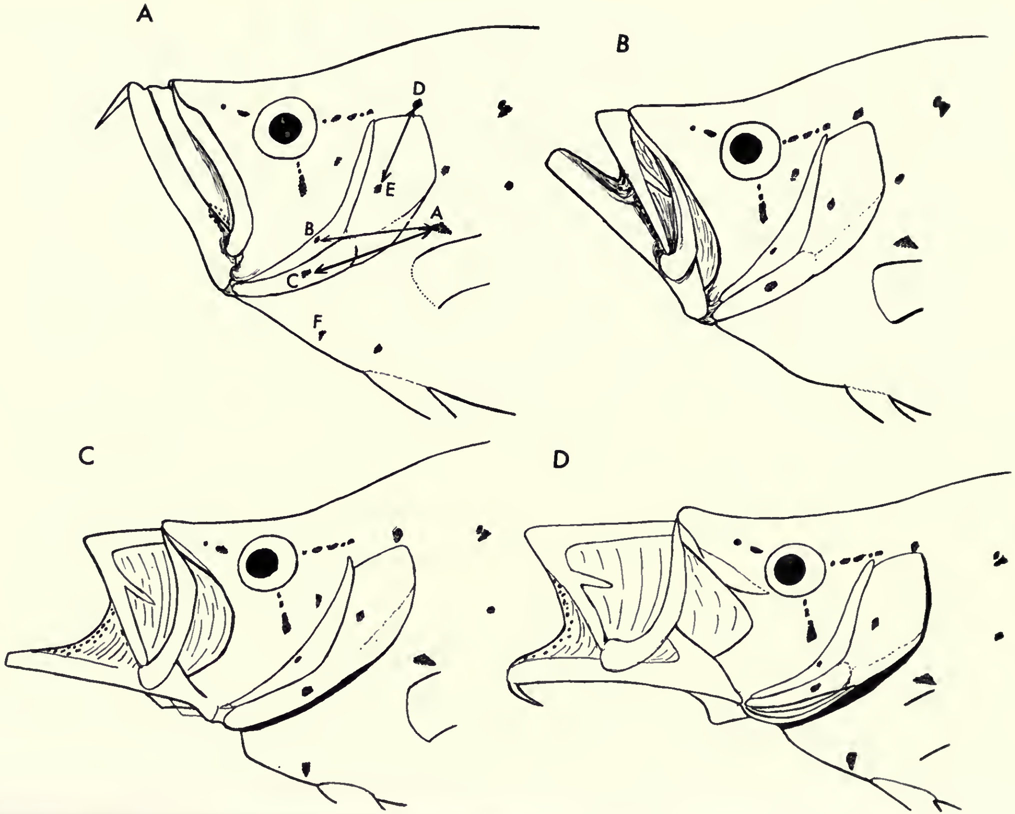
2. METHODS

Movement of the cranial components were recorded by motion pictures, utilizing the same technique as described by Liem (1967b). The recordings were made with a 16 mm. Arriflex reflex camera at speeds of 24–64 frames/sec. The films were analyzed with a LaFayette variable speed projector. Distances between various color markings and jaws are measured in successive prints and plotted graphically (Fig. 49). The horizontal axis of the graph represents frame number; the vertical axis indicates the distance between selected markings, the smallest distance being recorded as zero. Simultaneous recordings of lateral and ventral aspects of the head as made for *Helostoma* by Liem (1967b) have been omitted, because of the unpredictable angles between *Monocirrhus* and its prey.

Several surgical changes have been made on the ligaments of *Monocirrhus*. The fish was anesthetized with MS 222 (ethyl m-aminobenzoate methanesulfonate) using the standard procedure and dose. The ligaments mentioned in subsequent chapters were removed under water by cutting all attachments to the bones. After surgery, the fish was put in isolation in an aquarium. The fish recovered seemingly without any after-effects after 24 hours and attempted to feed within 48 hours.

3. MOTION ANALYSIS OF THE CAPTURE OF PREY BY UNANESTHETIZED *MONOCIRRHUS*

Monocirrhus captures prey in midwater by approaching the prey frontally and stealthily, and by sudden protrusion of both upper and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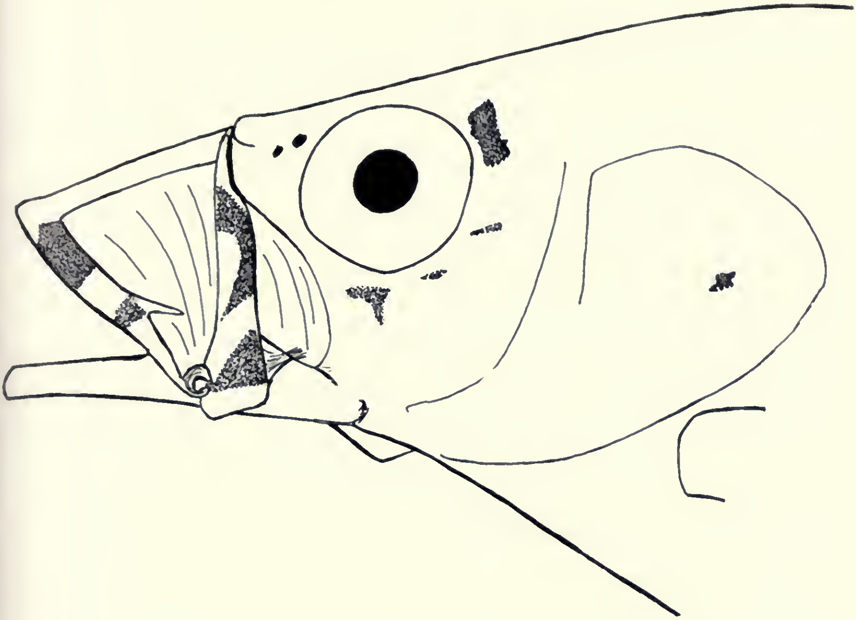

FIG. 47. Tracing of left side of head of photograph of *Nandus nebulosus* during maximal protrusion of jaws while feeding. Maxilla is straight and swung forward to a nearly vertical position. Gape of the mouth is directed somewhat ventrally. Urohyal is depressed and retracted and is visible below the quadratomandibular joint which is located straight below the eye.

lower jaws around the prey. The prey is always swallowed head first. The struggling prey is fixed in between the teeth of the jaws. *Monocirrhus* retracts its premaxillae with its jaws held firmly against the prey (Fig. 46). Then it swallows the prey by relaxing its grip, swimming forward for a very short distance, protruding its jaws, refixing its jaws further along the length of the prey, retracting its premaxillae, and repeating the sequence as often as necessary to swallow the prey. The swallowing process of large and elongate prey may last up to one hour.

FIG. 46. Tracings of individual frames of motion pictures of the lateral side of the head of *Monocirrhus polyacanthus* during feeding. A, Jaws are still fully adducted. Mouth is subvertical. Maxilla is oblique and parallel with ventral border of mandible. Letters and arrows indicate the distances between color markings used for motion analysis. B, Mandible is depressed slightly and the ventral end of maxilla has moved forward and ventrally. Premaxilla is not yet protruded. C, Mandible is depressed to nearly horizontal position and the maxilla is vertical. The mouth is completely open, but the premaxilla is protruded only partially. D, Mandible is fully depressed to a horizontal position. The maxilla is rotated forward and the premaxilla is completely protruded.

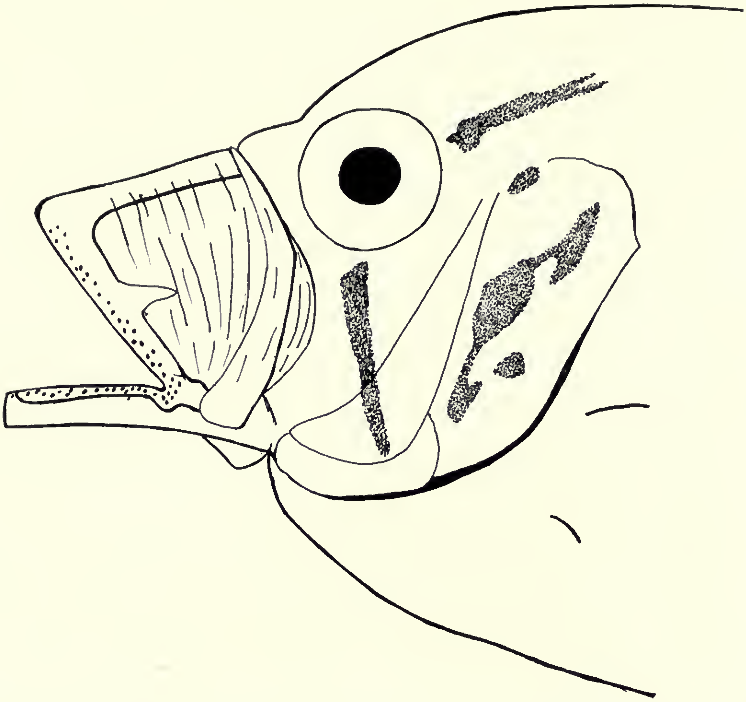

FIG. 48. Tracing of left side of the head of photograph of *Polycentrus schomburgkii* during maximal protrusion of jaws while feeding. Curved maxilla is swung forward in such a way that its distal end is located slightly anterior to its proximal end. Urohyal is visible just ventral to quadratomandibular joint, which is in a more cranial position than that of *Nandus*.

Figure 46 represents tracings of motion pictures. The motions are plotted graphically in Figure 49. Several important features can be read from these figures.

Protrusion of the premaxillae is always preceded by depression of the mandible. The lowering of the mandible initiates the protrusion of the upper jaw. Protrusion of the premaxillae proceeds in close correlation with further depression and protrusion of the mandible. The premaxillae are maximally protruded when the mandible is maximally depressed and protruded.

Protrusion of the premaxillae lags slightly behind the forward swinging of the distal portion of the maxillae. Maximal protrusion of the premaxillae occurs when the ventral end of the maxilla has swung forward maximally. Dorsally, the maxilla is restrained by the maxillonasal ligament.

Monocirrhus can protrude its premaxillae over a distance of more than one-third of the length of its head. However, only half of the length of the ascending process is protruded.

Dorsal rotation of the opercular is immediately followed by posterodorsal movement of the interopercular which, in turn, precedes the depression of the mandible (Figs. 46, 49).

Lowering of the mandible is accompanied by gradual lateral expansion of the suspensory apparatus and abduction of the mandibular rami at the symphysis.

After the initial stages of protrusion, the posteroventral movement of the urohyal becomes progressively more evident. The final stages of protrusion of both the upper and lower jaws are accompanied by maximal abduction of the suspensory apparatus and extreme posteroventral movement of the urohyal (Fig. 46).

A distinct cranial movement of the preopercular accompanies abduction of the suspensory apparatus.

No appreciable dorsal movement of the neurocranium has been recorded.

Once the prey has been captured head first between the jaws, the following movements in the head of *Monocirrhus* are recorded (Fig. 60). The jaws are very slightly adducted against the resistance of the prey. Retraction of the premaxillae takes place over one-sixth of the length of the head, while the mouth is open, the suspensory apparatus greatly abducted, and the urohyal retracted posteroventrally. Retraction of the premaxillae is preceded by a very slight backward swing of the ventral end of the maxilla. A slight elevation of the mandible occurs. In the next stage the fish loosens its grip by depressing the mandible and protruding the premaxillae over the same length as during retraction (one-sixth the length of the head). This is followed by retraction of the premaxillae. Protractory and retractory movements are repeated until the prey is transported to the pharynx. The posterior half of the prey is much narrower and retraction of the premaxillae occurs over a longer length and is accompanied by elevation of the mandible, partial adduction of the suspensory apparatus and protraction of the urohyal. Once the prey has been moved to the pharyngeal region, deglutition proceeds by movements of the branchial apparatus.

4. RESPIRATORY MOVEMENTS IN *MONOCIRRHUS*

Normal respiration in *Monocirrhus* proceeds without appreciable movements of the opercular. During quiet respiration *Monocirrhus*

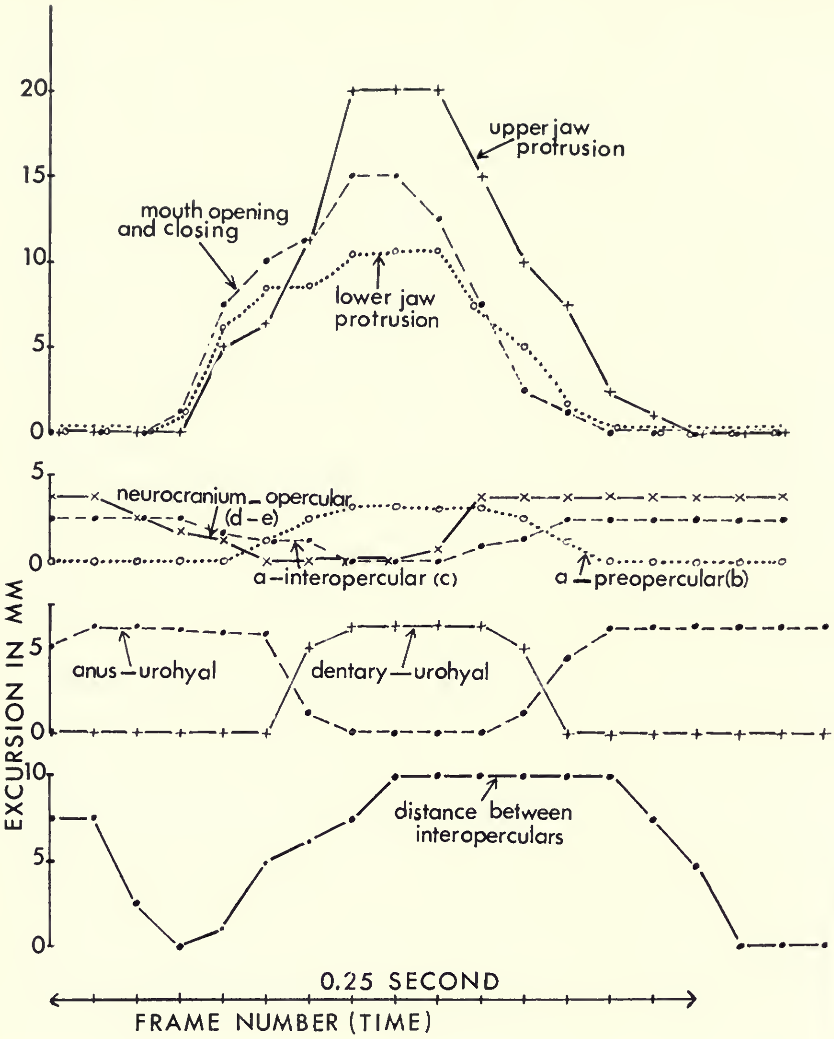

FIG. 49. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 8.1 cm.) during feeding under nearly natural conditions. Smallest distance between two elements is recorded as zero on vertical axis. Any deviation from zero is recorded as a positive figure on the vertical axis. Measurements are taken from successive frames. The horizontal axis represents successive frame numbers.

Upper graph: Broken line represents distance between anterior tip of upper jaw and anterior tip of mandible. Solid line represents distance between anterior tip of upper jaw and stationary point D in Figure 46a. Dotted line represents variations in the distance between the anterior tip of the mandible and stationary point A in Figure 46a.

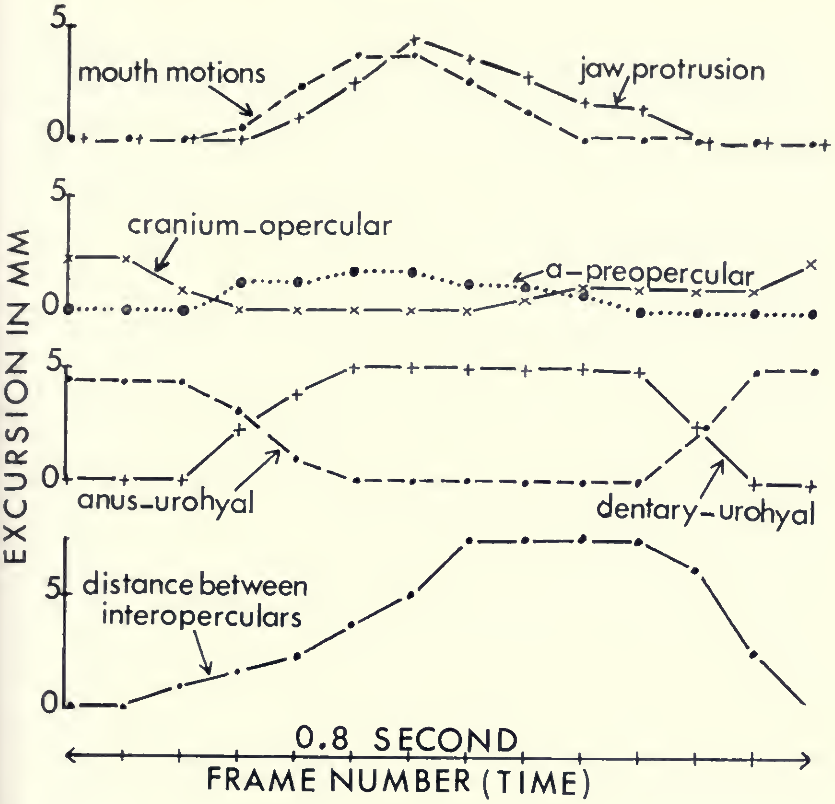

FIG. 50. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 7.9 cm.) during forced respiration. Opercular does not rotate. Abduction and adduction of opercular apparatus (bottom graph) are minimal. Further explanation in legend of Figure 49.

FIG. 49. *cont.*

Second graph: Solid line represents variations in distance between stationary point D and point E on the opercular in Figure 46a. Broken line represents variations in distance between stationary point A and point C on the interopercular in Figure 46a. Dotted line represents variations in distance between stationary point A and point B on the preopercular in Figure 46a.

Third graph: Solid line represents variations between urohyal and anterior tip of mandible from motion pictures of the ventral aspect of the head. Broken line represents variations in distance between anus and urohyal from motion pictures of the ventral aspect of fish.

Bottom graph: Represents variations in the distance between the interoperculars from motion pictures of the ventral aspect of the head.

depends mainly on the hyoid apparatus, which is instrumental in the "buccopharyngeal pressure pump mode" of respiration. Although very slight, the movements of the urohyal are visible. When breathing becomes more forceful by putting the fish in either oxygen-poor water or a urethane solution, the movements of the urohyal become more pronounced (Fig. 50). During inspiration the urohyal moves posteroventrally while the mouth opens slightly and the suspensory apparatus becomes abducted. Expiration proceeds by anterodorsal movements of the urohyal, adduction of the jaws, and adduction of the suspensory apparatus. Even during forceful respiration the opercular does not rotate but remains virtually stationary. Abduction and adduction movements of the opercular apparatus are minimal and coincide with identical movements of the suspensory apparatus. It is, therefore, clear that the opercular suction pump in *Monocirrhus* is not developed. The respiratory current across the gills is maintained by compression of the buccopharynx, by elevation of the hyoid apparatus and adduction of the suspensory unit without significant suction in the opercular cavity. It seems that the opercular apparatus has become incorporated into the specialized feeding apparatus and that it has become relatively independent of the respiratory functions.

5. RESPIRATORY MOVEMENTS IN OTHER NANDIDS

Observations have been made on *Nandus nebulosus* and *Polycentrus schomburgkii.* These species are very similar in their breathing mechanisms. During quiet respiration, no appreciable rotation of the opercular could be seen. However, the opercular apparatus was abducted and adducted rhythmically. During forceful respiration, the opercular apparatus was abducted to a much greater extent than in *Monocirrhus.* Active respiratory movements are performed by both the hyoid apparatus and opercular. However, the major respiratory mechanism seems to depend on the buccopharyngeal pressure pump. The opercular suction mechanism is relatively less active if compared with that of *Perca, Lepomis, Cichlasoma,* or *Pterophyllum.*

6. MOTION ANALYSIS OF *MONOCIRRHUS* WITH SURGICALLY-IMPAIRED LIGAMENTOUS SYSTEMS

Experiment a

The *interoperculomandibular ligaments* are completely removed from both sides. Observations have been made on five fish, all of which exhibit identical postsurgical behavior.

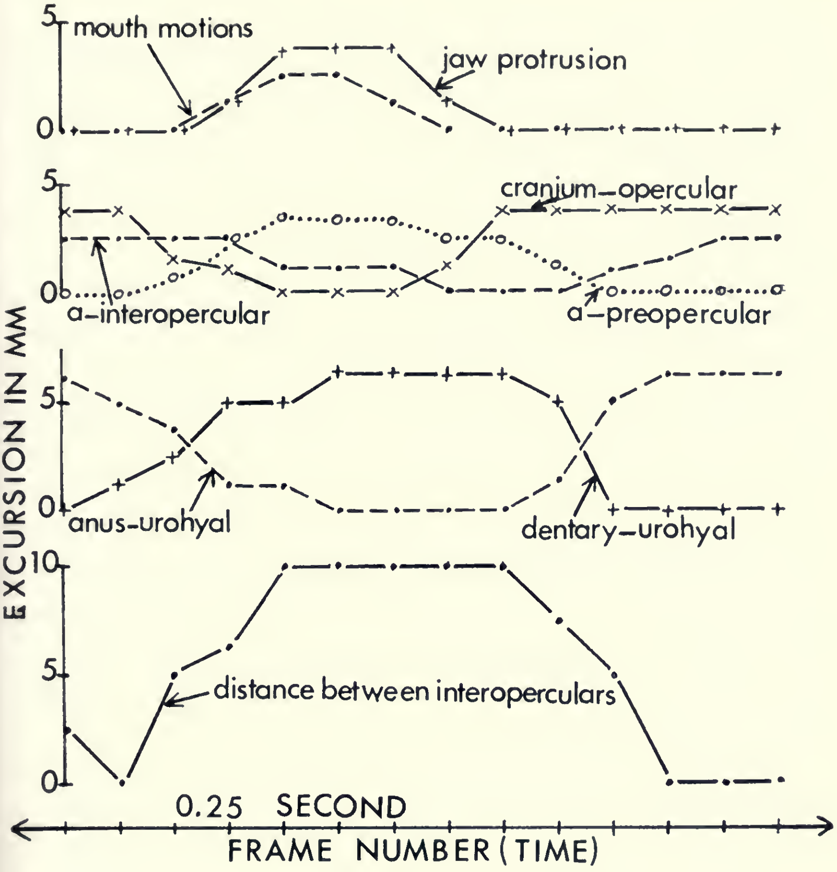

FIG. 51. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 7.9 cm.) with bilaterally removed interoperculomandibular ligaments during attempt to feed (*experiment a*). All motions proceed normally, except mouth opening and jaw protrusion. Further explanations in legend of Figure 49.

Respiration proceeds normally. The mandible is slightly depressed during pronounced abduction of the suspensory apparatus. Twenty-four hours after surgery the fish attempts to feed on live, albino *Clarias* sp. catfish of which the spines of the pelvic fins have been removed. The approach toward the prey is identical to that of the unanesthetized intact fish. However, the experimental fish are unable to capture their prey in numerous observed attempts. All five experimental fish died 11–24 days post-operatively of starvation. Intact *Monocirrhus* died after 9–35 days of starvation.

The inability of *Monocirrhus* with bilaterally-removed interoperculomandibular ligaments to capture prey is caused by the impaired mechanism to protrude and fully open the jaws. The fish can depress and protrude its mandible only to a very limited extent (Fig. 51). Depression of the mandible is preceded by extensive abduction of the suspensory apparatus. Depression of the mandible is followed by a slight forward swing of the ventral end of the maxillae, which, in turn, is followed by a slight protrusion of the premaxillae over a distance of one-sixth of the length of the head. Maximal protrusion of premaxillae and mandible never exceeds a distance of one-sixth of the length of the head in over 35 observations. Dorsal rotation of the opercular, posterodorsal movement of the interopercular, and posteroventral movement of the urohyal proceed normally. However, none of these movements are transmitted to the mandible in the absence of the interoperculomandibular ligaments.

Experiment b

The *interoperculo-opercular ligaments* are removed completely from both sides. Observations were made on three fish all of which exhibited identical movements of the head elements after surgery.

Respiration proceeds normally. The fish recovered within 48 hours. The experimental fish cannot capture their prey (guppies; albino, spineless *Clarias* sp.). The three fish died, respectively, 9, 17, and 21 days after surgery.

The bilateral removal of the interoperculo-opercular ligaments has a distinct effect on the protruding mechanism of the jaws. It seems to interfere with the initial phase of protrusion. The opercular rotates posterodorsally (Fig. 52), but this movement is not transmitted to the interopercular in the absence of the interoperculo-opercular ligament. The interopercular moves posterodorsally just after posteroventral movement of the urohyal. This is followed by depression of the mandible and forward swinging of the ventral end of the maxillary and partial protrusion of the premaxillae. The premaxillae are only protruded over a fourth of the length of the head. The experimental fish misses its prey invariably. The protruding mechanism seems too slow, especially during the initial stages of protrusion. The degree of protrusion is so limited that the experimental fish cannot catch disabled prey in numerous attempts.

Experiment c

The *interoperculohyoid ligaments* are removed completely from both sides. Observations are made on two fish.

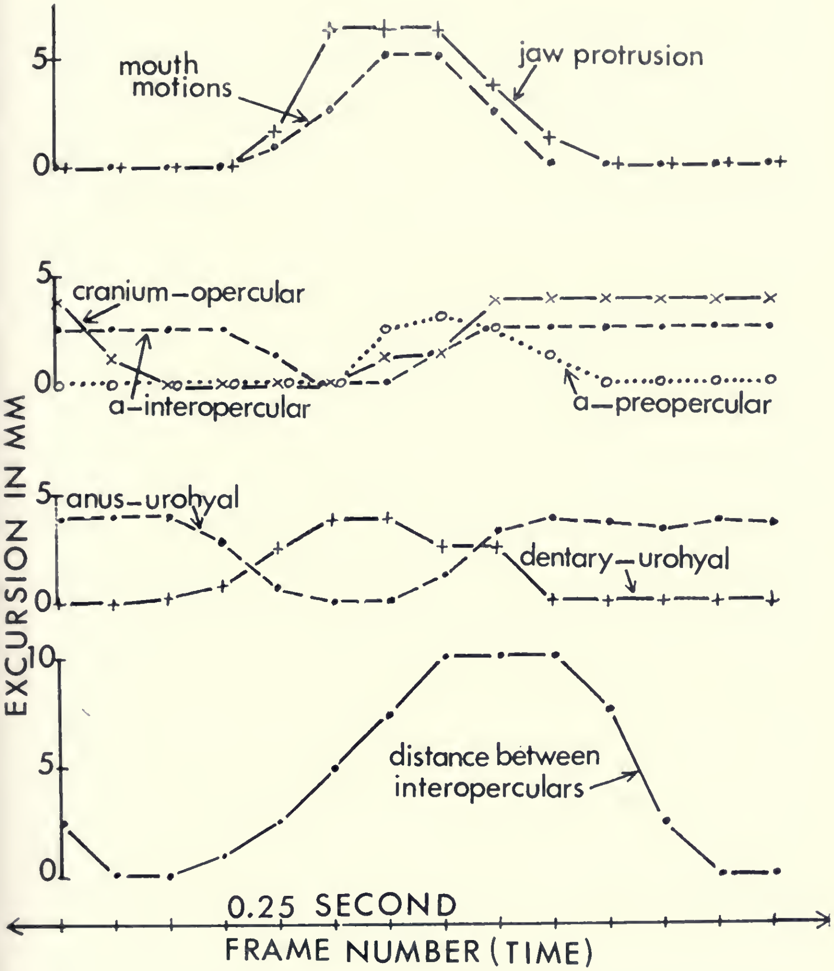

FIG. 52. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 8.3 cm.) with bilaterally removed interoperculo-opercular ligament during attempt to capture prey (*experiment b*). Movement of opercular is not transmitted to interopercular and affects the initial phase of mouth opening and jaw protrusion. Further explanation in legend of Figure 49.

Respiration proceeds normally. The experimental fish attempts to feed three days after surgery. However, both fish are unable to capture large prey, but small guppies, up to one-third the length of the experimental fish, are frequently caught. Jaw protrusion and mouth opening occur only to a limited extent (Fig. 53). It seems that the final stages of jaw protrusion do not occur as a result of the im-

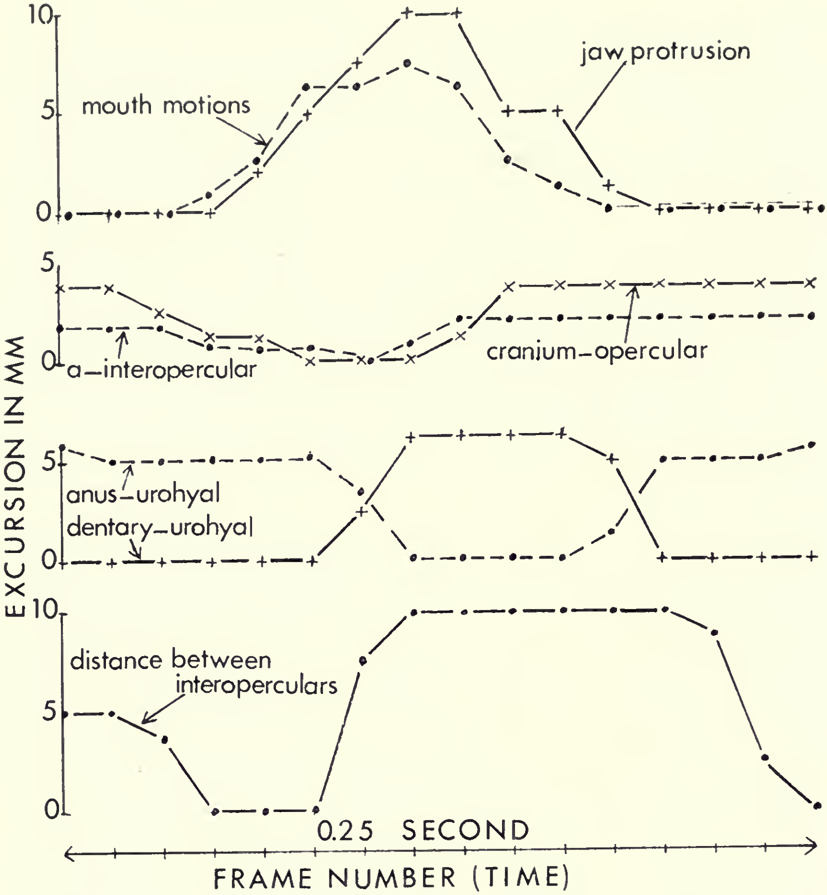

FIG. 53. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 8 cm.) with bilaterally removed interoperculohyoid ligaments during attempt to capture prey (*experiment c*). Posterodorsal motion of interopercular (a–interopercular in second graph) is more restricted and as a consequence the mouth opening and final stages of jaw protrusion are impaired. Further explanation in legend of Figure 49.

paired interoperculohyoid ligaments. However, the initial stages of protrusion proceed normally. The mandible is depressed partially, the ventral end of the maxilla swings forward to a limited extent and the premaxillae protrude over a length of slightly less than one-third of the head. With the impaired protractile apparatus the fish frequently misses the prey. However, small prey are occasionally engulfed and virtually inhaled in one stroke. The fish died, respectively, 39 and 91 days after surgery.

Depression of the lower jaw is always preceded by posterodorsal rotation of the opercular and posterodorsal motion of the interopercular. However, the degree of posterodorsal motion of the interopercular is more restricted than that of an intact fish (Figs. 49, 53). At the final stage of protrusion the premaxillae are protruded somewhat more during extreme abduction of the suspensory apparatus. The urohyal is drawn posteroventrally. However, the posteroventral motion of the hyoid apparatus is not followed by additional movement of the interopercular.

Experiment d

The thick, somewhat rounded, margin of the mouth is considered a lip (Fig. 45: LI). The lip extends between the anteroventral portion of the alveolar branch of the premaxilla and the anterodorsal tip of the dentary. Sections of 3 mm. are removed from the lip around both corners of the mouth. Observations have been made on two fish. Two other fish died immediately after surgery.

Respiration proceeds more forcefully. The fish try to feed two days after surgery. Only small guppies up to one-fourth the length of the experimental fish are occasionally caught. The fish died 49 and 79 days, respectively, after surgery.

Jaw protrusion and depression of the mandible are impaired. The initial stages of jaw protrusion seem to proceed in a pattern similar to that in intact fish (Figs. 49, 54). However, in the later stages of protrusion, the mandible is depressed and protruded to a full extent, while the premaxillae remain stationary in a partially protruded position (Fig. 54). The maxillary is swung forward to the same extent as in intact fish. However, downward movement of the mandible does not seem to be transmitted directly to the premaxilla as in intact fish. Opercular rotation, interopercular and preopercular movements, retraction of the hyoid, and abduction of the suspensory apparatus proceed normally.

Closure of the jaws seems to proceed normally. However, during respiration there is a leakage of water through the gaps at the corners of the mouth and the fish compensates by more forceful respiration.

Experiment e

Both *medial* and *anterior maxillomandibular ligaments* are removed from both sides. I have not been able to remove the individual ligaments separately. Observations have been made on two fish. Three fish died shortly after surgery.

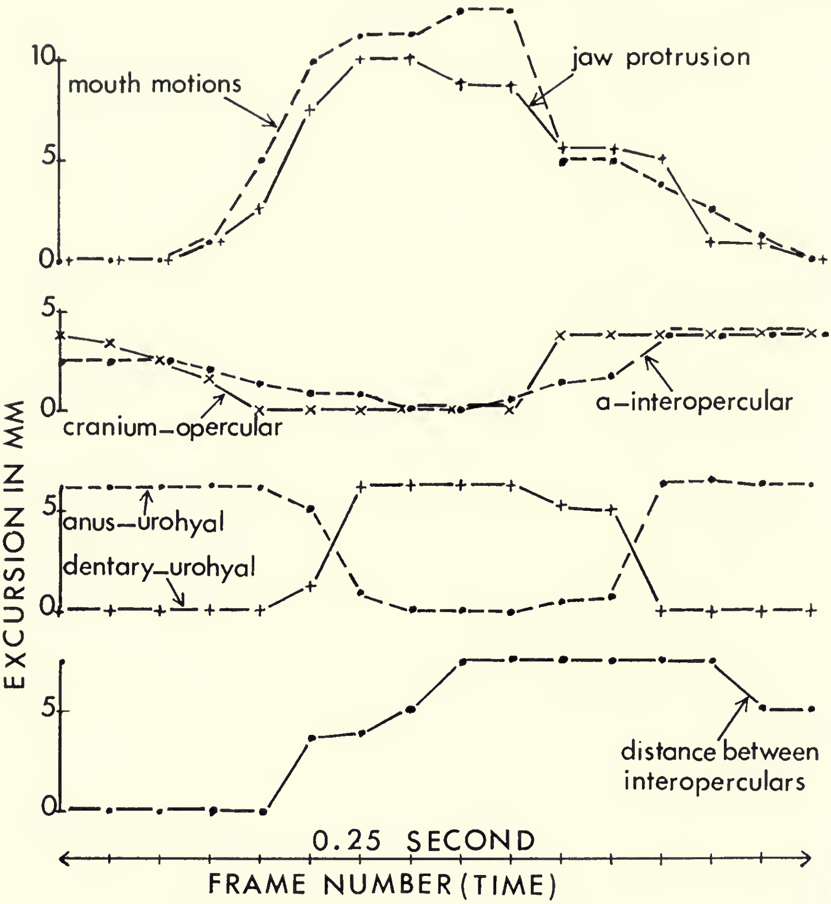

Fig. 54. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 7.7 cm.) with bilaterally interrupted lips, during attempt to capture prey (*experiment d*). Most movements proceed normally, even the initial stages of mouth opening and closing. In the final stages the mandible is fully depressed and protruded, but premaxillae remain only partially protruded. Further explanation in legend of Figure 49.

Respiration proceeds normally. The fish try to feed three days after surgery. Neither of the two experimental fish is able to capture its prey. The fish died 11 and 15 days, respectively, after surgery.

Depression of the mandible proceeds nearly normally (Fig. 55). The mouth opens partially. The premaxillae are not protruded in the initial stages and the maxilla rotates only very slightly. When the mandible is depressed fully in the final stages of protrusion, the premaxillae are protruded over a distance of slightly less than one-

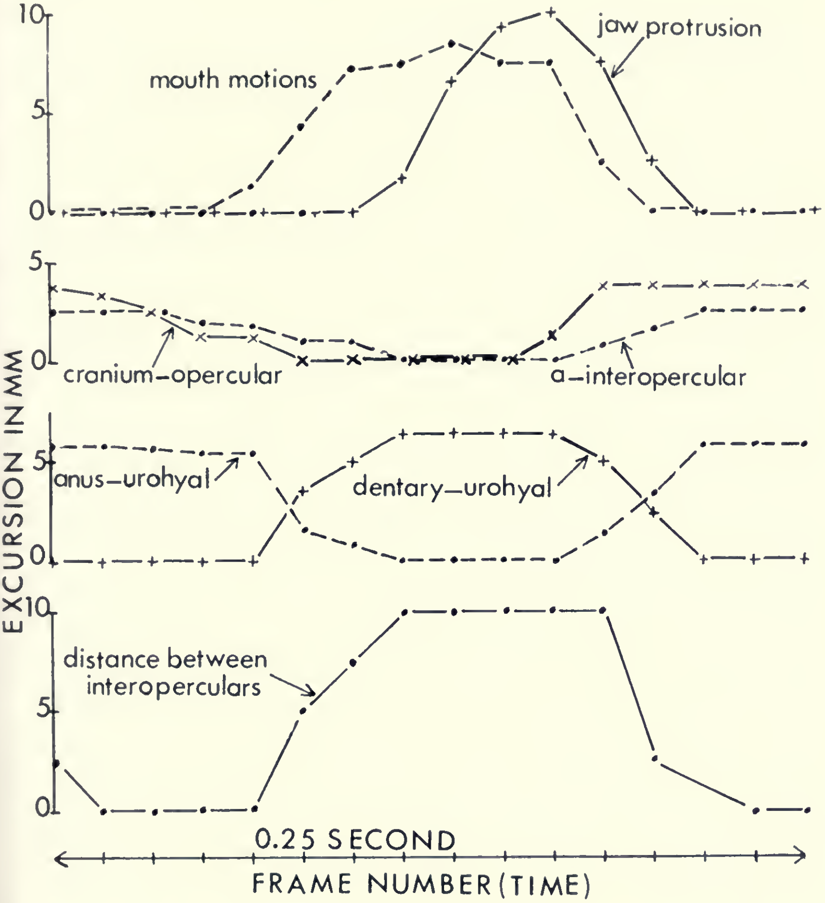

FIG. 55. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 8.2 cm.) with bilaterally removed medial and anterior maxillomandibular ligaments during attempt to capture prey (*experiment e*). Most movements proceed normally. Initial phase of jaw protrusion does not take place although mandible is depressed normally. Depression of mandible is transmitted to premaxillae in final stages of the cycle. Further explanation in legend of Figure 49.

fourth of the length of the head. The maxilla rotates with the movement of the premaxilla.

Rotation of the opercular, posterodorsal movement of the interopercular, retraction of the hyoid, and abduction and protraction of the suspensory apparatus proceed normally (Fig. 55).

Closure of the jaws is somewhat impaired. When the prey is caught between the jaws, it invariably escapes. The removal of the ligaments between the mandible and the maxilla seems to eliminate the necessary stability from the adductor apparatus. During both quiet and forceful respiration the jaws can be closed completely against the resistance of the water.

Experiment f

The *tendon of the adductor mandibulae muscle* is cut from the head of the maxilla on both sides. None of the five experimental fish survived longer than seven hours after surgery. Observations have been made on only three anesthetized fish.

Respiration seems to be impaired. The mouth remains partially open. The loss of tension in the tendon of the adductor mandibulae renders the muscle totally ineffective. The movements of the hyoid and suspensory apparatus are very pronounced. Retraction of the hyoid apparatus opens the mouth and protrudes the premaxillae over a distance of about one-fourth the length of the head. Once the premaxillae and mandible are protruded, they remain stationary. The respiratory current created with partially opened and protruded jaws seems insufficient to maintain life. Suspended particles of dried fish food around the mouth are sucked into the mouth during posteroventral movement of the hyoid and abduction of the suspensory apparatus. However, the particles are expelled with the water stream from the mouth during anterodorsal movement of the hyoid apparatus and adduction of the suspensorium. The opercular apparatus does not participate in the respiratory movements. No observations have been made on feeding, since none of the fish with severed tendons of the adductor mandibulae muscles survived for longer than seven hours.

Experiment g

The *interhyals* are removed completely from both sides. Observations have been made on two fish, exhibiting identical post-surgical behavior.

Respiration proceeds normally. The mandible is slightly depressed during pronounced abduction of the suspensory apparatus. Forty-eight hours after surgery the fish attempts to feed on live

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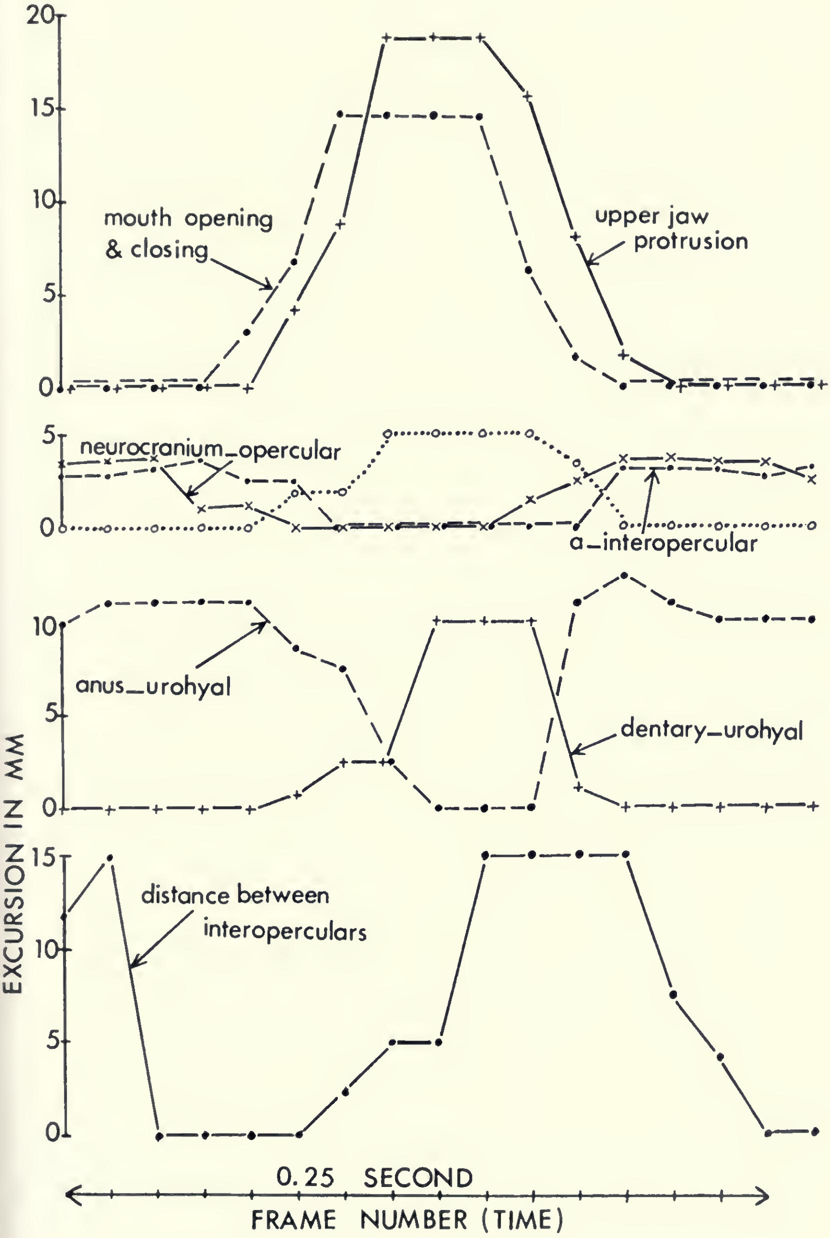
FIG. 56. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 8.1 cm.) with bilaterally removed interhyals during attempt to capture prey (*experiment g*). Most movements proceed normally as in intact fish. Abduction of the suspensory apparatus (bottom graph) is more pronounced. Posterior displacement of urohyal is greatly augmented (third graph). Further explanation in legend of Figure 49.


20
15
10
5
0
mouth opening & closing
upper jaw protrusion
5
0
neurocranium_opercular
a_interopercular
10
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dentary_urohyal
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distance between interoperculars
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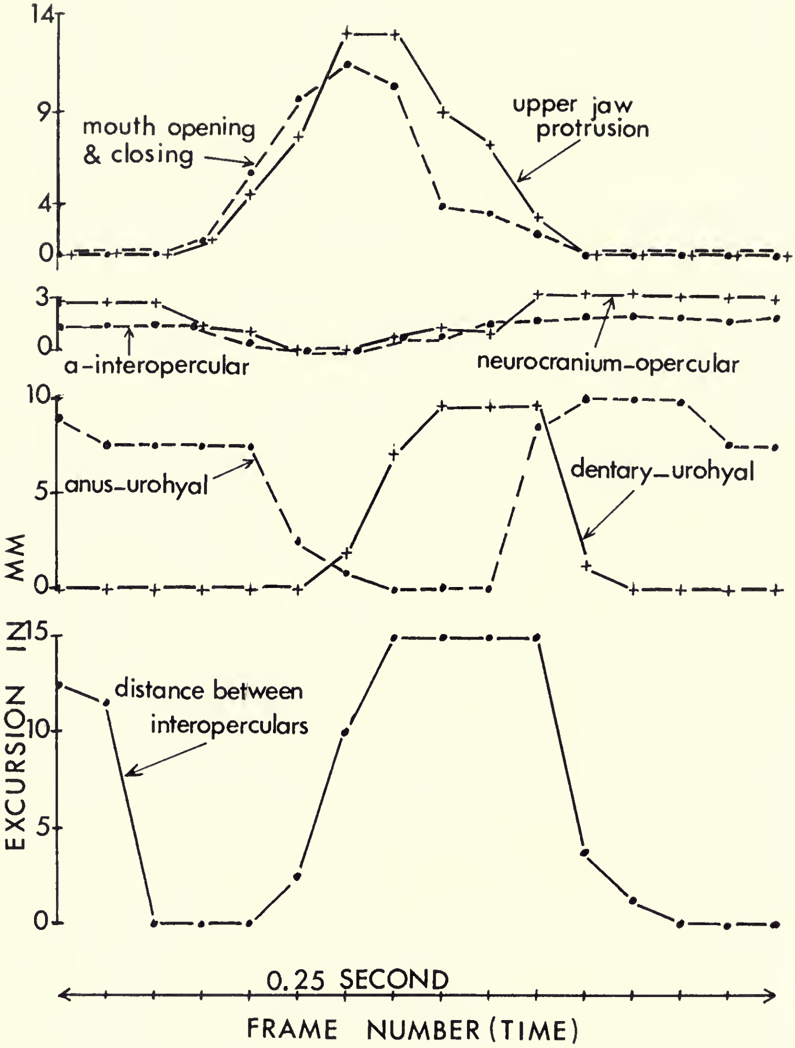

FIG. 57. Graphic representation of motions of bony elements in the head of *Monocirrhus polyacanthus* (total length 7.9 cm.) with the urohyal separated from the rest of the hyoid apparatus (*experiment h*). Jaw protrusion and mouth opening occur only to a limited extent. The suspensory apparatus is greatly abducted. Further explanation in legend of Figure 49.

prey. The approach toward the prey is identical to that of the unanesthetized fish. The fish made numerous successful attempts to capture prey. The fish lived for 61 and 40 days, respectively, after surgery.

The pattern of movements of the cranial elements during feeding of the experimental fish (Fig. 56) resembles that of intact fish (Fig. 49) very closely. However, abduction of the suspensory apparatus (expressed by the distance between the interoperculars from a ventral aspect) seems more pronounced, although of somewhat shorter duration (bottom graph of Fig. 56). The posterior displacement of the urohyal, which represents the posterior movement of the hyoid apparatus is greatly augmented (third graph of Fig. 56). The movements of the interopercular, opercular, preopercular, maxilla, premaxilla, and mandible proceed normally. The effects of removal of the interhyals seem, therefore, to be minimal on the functions of the jaw and hyoid apparatus.

Experiment h

The connection between the *urohyal* and the rest of the hyoid apparatus has been severed, and the anterior end of the urohyal dissected free. Observations have been made on two fish.

Respiration appears impaired. The mouth opens partially during extreme abduction of the suspensory apparatus. Extreme abduction of the suspensory apparatus is followed by abduction of the opercular apparatus. The experimental fish seems to compensate for the loss of the pressure pump mechanism by ventilating at a higher rate and relying on abduction-adduction movements of the suspensorium and opercular apparatus. The fish attempt to feed three days after surgery. However, both fish are unable to capture prey, even of small size. The fish died 7 and 13 days, respectively, after surgery.

Jaw protrusion and mouth opening occur only to a limited extent (Fig. 57). It seems that the final stages of jaw protrusion do not occur. However, the initial stages of protrusion proceed normally. The mandible is depressed partially, the ventral end of the maxilla swings forward and the premaxillae protrude over a distance of slightly less than one-third the length of the head. Depression of the mandible is always preceded by posterodorsal rotation of the opercular and a slight posterodorsal movement of the interopercular. At the final stage of protrusion the suspensory apparatus is greatly abducted. Abduction of the suspensory apparatus proceeds normally.

Functional Morphological Analysis

This analysis is based on the morphology of the bones, joints, ligaments, muscles, and motion analysis of intact fish and fish with surgically-modified ligamentous systems. The only functions considered are respiration and feeding. Many authors (e.g., Willem, 1931; Woskoboinikoff, 1932; Alexander, 1967; Liem, 1967b) have found that in general there are great similarities in the chronological relationships and nature of the movements of the cranial elements during feeding and respiration. However, all authors have reported far greater amplitudes of movements during feeding.

The salient features during respiration and feeding are opening and closing of the jaws, protrusion of the jaws, volume and pressure variations in the buccopharyngeal cavity, abduction and adduction of the opercular apparatus, and complex movements of the gill arches. However, all these functions are mutually interdependent and should not be considered separately. Liem (1967a, b) has proposed to treat the neurocranium, suspensory apparatus, jaw apparatus, opercular apparatus, hyoid apparatus, pectoral girdle, and branchial basket as independent mechanical entities and he has named each entity a functional unit. Gans (1969) has discussed the ambiguity of Liem's interpretation of functional unit originally proposed by van der Klaauw (1945). Gans suggested that mechanical unit, i.e., assemblage of structural elements that share limited degrees of internal movement, would be a better descriptive term. Ballintijn and Hughes (1965) and Liem (1967a, b) have recognized that two or more mechanical units are often connected to form a coupling, which performs a specific function within the feeding and respiratory apparatus. The concept—coupling—may not always be applicable in higher vertebrates, but it seems to play a very major role in teleosts. The subdivision of the skull into mechanical units is diagrammatically represented in Figure 58.

1. THE LEVATOR OPERCULI-OPERCULAR APPARATUS-MANDIBLE COUPLING

The existence and functioning of this coupling can be determined from motion analysis of the feeding movements of the intact fish

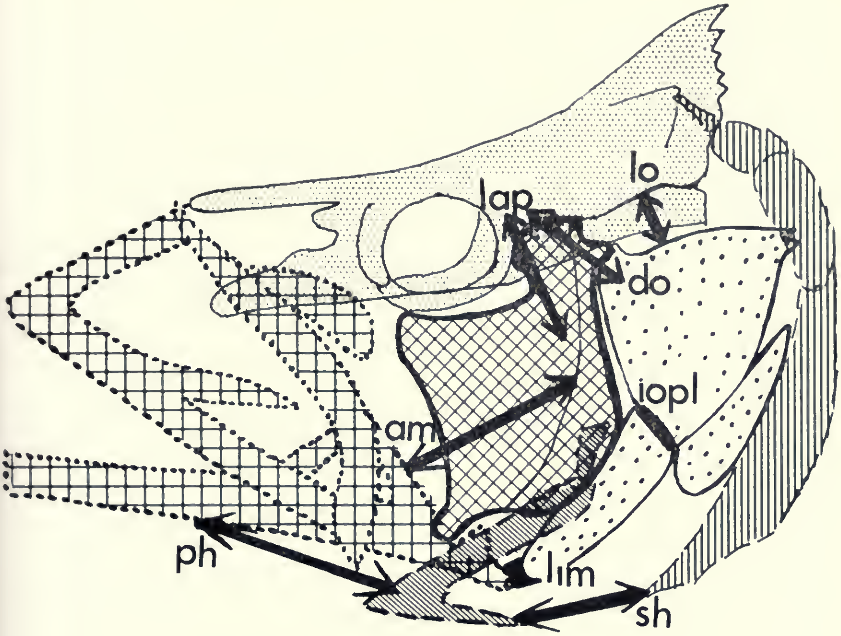

FIG. 58. Diagram of major functional units and cranial musculature of the nandid head. Arrows indicate main fiber or tendon direction of the muscles. Ligaments are in solid black. Lightly stippled area is neurocranium; obliquely cross-hatched area is suspensory apparatus; perpendicularly cross-hatched area is jaw apparatus; heavily stippled area is opercular apparatus; finely and obliquely lined area is hyoid apparatus; heavily and vertically lined area is pectoral girdle; AM, adductor mandibulae; DO, dilator operculi; IOPL, interoperculo opercular ligament; LAP, levator arcus palatini; LIM, interoperculomandibular ligament; LO, levator operculi; PH, protractor hyoideus; SH, sternohyoideus.

(Fig. 49). When the distance between the neurocranium and opercular becomes smaller, the interopercular moves dorsally. The motion of the interopercular initiates the opening of the mouth. No other movement can be so well correlated with the opening of the jaws. Caudal movement of the hyoid and cranial movement of the preopercular occur after the mouth has opened partially. The only possible conclusion is that opening of the mouth is initiated by the following events, representing the functioning of the levator operculi-opercular apparatus-mandible coupling (Fig. 58). Contraction of the levator operculi muscle will rotate the opercular around the operculo-hyomandibular joint. This motion is transmitted directly to the interopercular by the operculo-interopercular ligament. The nearly vertical interopercular will pull the posteroventral corner of the mandible dorsally via the nearly vertical interoperculomandibular ligament. Since this dorsal pull is applied posteroventrally to the quadratomandibular joint the anterior tip of the mandible will move ventrally, opening the mouth. This coupling results in a vertical, dorsally-directed force, rather than a horizontal posteriorly-directed force on the posteroventral corner of the mandible. The subopercular is excluded from this coupling by the differentiation of a direct ligamentous connection between opercular and interopercular. The action of this coupling can be interrupted by removal of the operculo-interopercular ligaments (Fig. 52, experiment b). The movement of the opercular elicited by contraction of the levator operculi muscle is not transmitted to the interopercular (graph 2, Fig. 52). The posterodorsal movement of the interopercular does not take place in the beginning of the mouth opening cycle. The mouth opens at a later stage of the cycle after the posteroventral movement of the hyoid, which draws the interopercular posterodorsally via the interoperculohyoid ligament. The inactivity of the levator operculi-opercular apparatus-mandible coupling limits the opening of the mouth and jaw protrusion significantly, although the movements of the opercular, hyoid apparatus and suspensory apparatus (Fig. 52) are comparable with those of the control experiment (Fig. 49). The levator operculi-opercular apparatus-mandible coupling initiates the opening cycle of the jaws since the beginning cycle always occurs even when other couplings have been interrupted (Figs. 53, 54, 56). Interruption of the levator operculi-opercular apparatus-mandible coupling impairs the jaw mechanism permanently.

2. THE STERNOHYOID–HYOID–INTEROPERCULAR–MANDIBLE COUPLING

This coupling can be deduced from the control experiment (Fig. 49). Maximal jaw opening and protrusion is always preceded by a posteroventral movement of the urohyal (Fig. 49, third graph). The posteroventral movement of the urohyal can be caused by contraction of the sternohyoid muscle (Fig. 58). In graph 2 of Figure 49 we see that the most posterodorsal position of the interopercular coincides with maximal protrusion of the upper jaw and depression of the mandible. Because the interopercular is connected to the epihyal (Fig. 36) and opercular rotation has attained its maximum posterodorsal position two frames before maximal protrusion of the upper jaw, we have to eliminate the possibility that maximal protrusion is caused by opercular rotation. The continued posterodorsal movement of the interopercular must, therefore, be caused by the posterior movement of the hyoid. This posterior movement is transmitted to the interopercular by the interoperculo-hyoid ligament. This coupling involves contraction of the sternohyoid and posteroventral movement of the hyoid, which is transmitted to the interopercular by the interoperculohyoid ligament, followed by the posterodorsal movement of the interopercular, resulting in a posterodorsal force on the mandible posterior and below the quadratomandibular joint, through the interoperculomandibular ligament, causing the partially-depressed mandible to drop. The existence of this coupling can be demonstrated by removing the interoperculohyoid ligaments (experiment c, Fig. 53). The only effects elicited by the impairment of the sternohyoid-interopercular-mandible coupling is the limited extent of the posterodorsal movement of the interopercular, the short duration of the posterodorsal position of the interopercular, and the elimination of the last stage of jaw protrusion. The upper jaw is not fully protruded (Figs. 53, 54), while the mandible is depressed only partially, despite the normal movements of the opercular, hyoid, and suspensory apparatus. The initial phases of jaw protrusion and mouth opening seem to be normal, indicating that the levator operculi-opercular apparatus-mandible coupling initiates jaw protrusion and mouth opening. The impaired final stages in experiment c suggest that the sternohyoid-hyoid-mandible coupling is responsible for final and full jaw protrusion.

3. THE SUSPENSORY ABDUCTORS–SUSPENSORY APPARATUS–MANDIBLE COUPLING

The functions of the two couplings discussed under parts 1 and 2 of this chapter depend on the interoperculomandibular ligament (Figs. 33, 58: LIM). In experiment a the interoperculomandibular ligaments have been removed bilaterally, so that the functions of both couplings are abolished. The effects of this experiment are quite pronounced (Fig. 51). Jaw protrusion and mouth opening are greatly impaired despite the normal movements of the opercular, interopercular, hyoid, and suspensory apparatus. This proves that the interoperculomandibular ligament is absolutely essential for the proper functioning of the jaw apparatus. However, the jaw is still protruded and opens slightly (Fig. 51). In graph 2 of Figure 51 we see that the preopercular is protracted, i.e., moves anteriad. This forward motion of the preopercular and consequently the entire suspensory apparatus is always correlated with abduction of the suspensory apparatus

(Figs. 49, 51, 52, 56). Protraction of the suspensory apparatus is either simultaneous with or preceded by suspensory abduction. The levator arcus palatini muscle is the principal abductor of the suspensory apparatus (Figs. 33, 58: LAP). However, abduction is always accompanied by slight protraction of the suspensory apparatus (Figs. 49, 52, 56). Therefore, the levator arcus palatini acts secondarily as a protractor of the suspensorium. Protraction of the suspensory apparatus may act directly on the jaw apparatus by bringing it forward, i.e., slight protrusion. Slight opening of the mouth is the result of extreme abduction of the suspensory apparatus (Fig. 50). The quadratomandibular joint is a modified saddle joint (Fig. 59) and only one set of articular surfaces is in close contact at any one position of the suspensory apparatus. When the suspensory apparatus is adducted the lateral head of the quadrate is in close contact with the lateral horizontal fossa of the angular. When the suspensory apparatus is abducted and slightly protracted, the lateral head of the quadrate rolls out of the lateral horizontal fossa and the medial articular head rotates and rolls into the medial vertical fossa of the angular. During rotation and rolling, a downward force is exerted by the medial articular head on the lateral wall of the medial vertical fossa. This will depress the mandible slightly. When the mandible is depressed, the medial articular head of the quadrate fits snugly into the medial vertical fossa of the angular. The morphological characteristics of the joint, the rolling and rotation of the medial articular head of the quadrate during abduction of the suspensory apparatus, are instrumental in the functioning of the suspensory abductors-suspensory apparatus-mandible coupling.

4. MOVEMENTS OF THE JAW APPARATUS

Gosline (1966) in reviewing percoid fishes stated: ". . . rotation at the anterior end of the maxillary causes protrusion of the premaxillaries. . . ." Alexander (1967) concludes that the screw movement of the maxillae causes the protrusion of the premaxillae. These alleged generalizations for acanthopterygian fishes are not applicable to either the nandids or labrids (Hasselt, 1968).

During normal feeding movements, protrusion of the premaxillae is always preceded by depression of the mandible (Fig. 49). In the initial stages of mouth opening the maxilla swings forward without the rotation or screw movement, yet the premaxillaries are protruded. This suggests that the screw movement or rotation of the maxillae does not cause protrusion of the premaxillae in the acanthopterygian

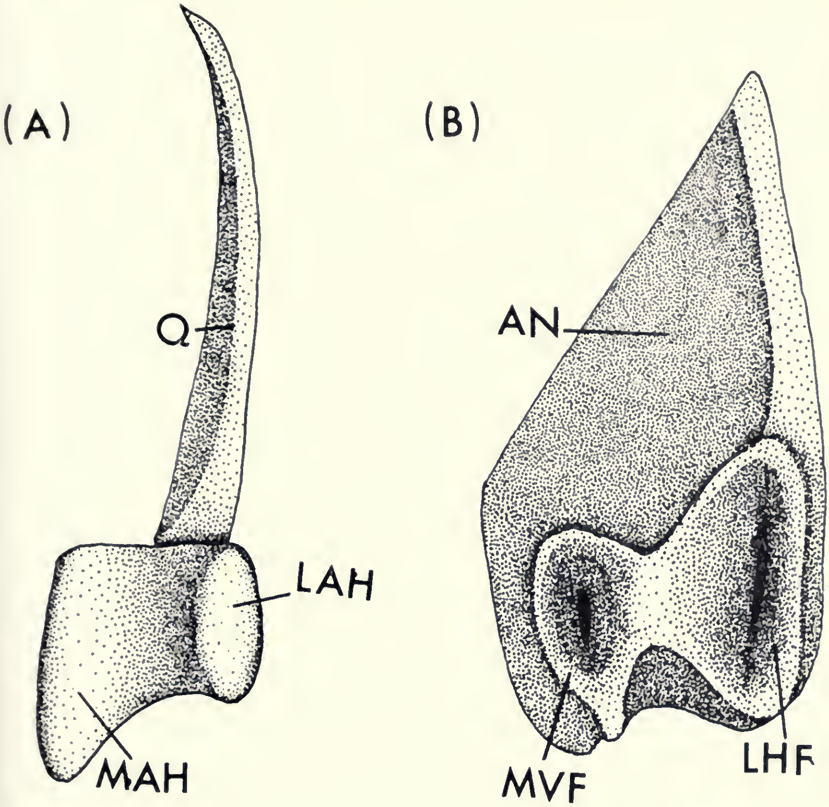

FIG. 59. A, Ventral view of the quadrate of *Monocirrhus polyacanthus*. B, Dorsal view of angular (articular). AN, angular; LAH, lateral articular head of quadrate; LHF, lateral horizontal fossa of angular; MAH, medial articular head of quadrate; MVF, medial vertical fossa of angular; Q, quadrate.

family, Nandidae. In nandids protrusion of the premaxillae is a function of depression of the mandible. When the mandible is depressed, the medial and anterior maxillomandibular ligaments pull the ventral ends of the maxillae forward and laterally. The maxillae undergo the swinging and screw movement passively. The medial and anterior maxillomandibular ligaments connect the ventral ends of the premaxilla and maxilla to the ascending process of the dentary (Fig. 45). When the mandible is depressed, the medial and anterior maxillomandibular ligaments pull the ventral ends of the premaxillae forward and slightly downward causing the protrusion of the upper jaw. Interruption of the medial and anterior maxillomandibular ligaments (experiment e, Fig. 55) will eliminate the ventrocraniallydirected pulling force on the ventral ends of the premaxillae. The beginning stages of jaw protrusion do not occur, although the mandible is depressed and the maxilla undergoes a forward swing followed by a screw movement. Upper jaw protrusion does occur in this experiment after extreme depression of the mandible. The principal structure involved in the final stages of jaw protrusion is the lip. When the mandible is depressed over a large distance, the lip (Figs. 45, 46) becomes taut and pulls the premaxillae forward. In experiment d (Fig. 54) the lip has been interrupted. The initial stages of jaw protrusion proceed normally, but the premaxillae remain stationary in a partially-protruded position (Fig. 54), while the mouth continues to open. The maxillae swing forward and undergo normal rotation. These screw movements of the maxillae do not affect the partially protruded, but stationary premaxillae. This conclusively proves that the screw movement of the maxillae does not cause protrusion of the premaxillae in nandids.

The mechanism underlying jaw protrusion in nandids can be summarized as follows: Lowering of the mandible will cause a tension in the medial and anterior maxillomandibular ligaments, which pull the ventral ends of the premaxillae forward and slightly downward. In the final stage of jaw protrusion, the lip pulls the premaxilla in its extreme forward position. The temporal sequence of these two mechanisms can be postulated from experiments d and e (Figs. 54, 55). A similar mechanism has been described for the Gerridae (mojarras) by Schaeffer and Rosen (1961).

The maxilla in nandids functions as a brace, stabilizing the adductor apparatus. Removal of the attachments of the maxilla to the mandible (experiment e) will cause the experimental fish to loose its grip on the captured prey. The portion of the medial maxillomandibular ligament associated with the maxilla performs an important function in realizing the major role of the maxilla as the principal support or brace of the adductor apparatus.

The absence of the "screw movement of the maxillary mechanism" as postulated by Alexander (1967) can also be deduced morphologically. The morphological prerequisite for the screw mechanism is the presence of the articular process of the premaxilla. Pressure of the premaxillary condyle of the maxilla on the articular process of the premaxilla causes the protrusion of the premaxilla. However, the articular process of the premaxilla is absent in nandids and in the majority of percoid families. The "screw movement of the maxillary mechanism" does not occur in the majority of percoid families because of the absence of the articular process of the premaxilla.

The length of the ascending processes of the angular and dentary has been explained in terms of torque. Progressive increase in height of the ascending process of the dentary (coronoid process) results in a geometric increase in torque (Schaeffer and Rosen, 1961; Matthes, 1963; Liem, 1967b). However, in the majority of percoids the adductor mandibulae muscles do not insert on the ascending process of the dentary, but, as in nandids (Figs. 31, 33, 44, 45), on a common tendon of the intramandibularis muscle ventral to the ascending process of the dentary. An alternate explanation for the adaptive significance of the increased height of the ascending process of the dentary should be sought in relation to the functions of the medial and anterior maxillomandibular ligaments. The greater the lengths of the ligaments, the greater the slack, which affects the speed and degree of movements of the connected parts. The increased height of the ascending process of the dentary will shorten the distance between the dentary, premaxilla, and maxilla. This distance is bridged by the medial and anterior maxillomandibular ligaments, which are very short and have minimal slack in nandids and other percoids with long ascending processes of the dentary. The adaptive significance of the ascending process of the dentary (coronoid process) is best explained in terms of reducing the slack in the medial and anterior maxillomandibular ligaments and of increase in speed and efficiency of the transformation of the movement of the mandible to the upper jaw.

The lengths of the jaws in nandids are extraordinary. Gosline (1966) states that long jaws militate against biting down on anything with much force since the partly rotated maxillaries do not form a very firm support for the lateral ends of the premaxillaries. However, nandids can hold large, struggling prey for extended periods. The strong maxillomandibular ligaments will enable the rotated maxillae to function as strong braces. Protrusion of the premaxillae will be ineffective in capturing prey or in feeding by engulfing nearby objects if it is not accompanied by an equivalent protrusion of the lower jaw. Protrusion of the mandible as a result of the suspensory abductors-suspensory apparatus-mandible coupling is negligible (Figs. 50, 57). The long mandible when adducted, is nearly vertical (Fig. 46, A). When it is lowered, the anterior tip moves forward in a circular movement around the quadratomandibular joint. The anterior tip of the mandible will move forward in a co-ordinated manner with the anterior tip of the premaxillae in protrusion. During maximal protrusion of the premaxillae, the mandible reaches a horizontal position with its anterior tip in the most extreme forward position (Fig. 46, D) corresponding with the most craniad position of the anterior tip of the upper jaw. "Protrusion" of the mandible is nothing else than a rotation of the subvertical mandible around the quadratomandibular joint into a horizontal position. The degree of "protrusion" of the lower jaw is directly proportional to the length of the mandible. Percoids with long ascending processes of the premaxillae, and, therefore, highly protrusible premaxillae, have correlated long mandibles. Elongate jaws increase both the speed and grasping range of the bite, which are essential adaptations in predation.

5. ABDUCTION OF THE SUSPENSORY APPARATUS

Abduction of the suspensory apparatus is brought about by the levator arcus palatini muscles (Ballintijn and Hughes, 1965) and the sternohyoideus muscle (Henschel, 1941). Gosline (1966) has subdivided the percoids into two major subdivisions. In one group, the levator hyomandibulae (levator arcus palatini) is small, resulting in limited abduction and in the second group the muscle is large, resulting in greater expansion of the buccopharynx. This generalization, based on casual observations of muscle size in fixed material is invalid. Gans and Bock (1965) have demonstrated convincingly that muscle size has no relationship with degree of movement and strength. One cannot make any conclusions on the size of muscles in material fixed under various conditions. Many other parameters, e.g., fiber length, moment arm, fiber angulation, tendons, play an important role in muscle function. Muscle size should be compared by dry weight (Scapino, 1968) or volume (Schumacher, 1961).

Van Dobben (1937), Henschel (1941), and Ballintijn and Hughes (1965) have shown that the force produced by the sternohyoideus muscle along the rami of the hyoid can be resolved into two components: one abducting the interopercular and, through the stylohyal, the palatal complex; the second component results in a caudal movement of the interopercular. Gosline (1966) applied this theory to the percoid fishes and he distinguished two major groups. In one group, the hyoid rami are only two-thirds as long as those of the second group, so that the lateral expansion of the suspensory apparatus is only two-thirds as great. This assumption can be true only if there is no resistance in changes of the angle at the joints that unite the two hyoid bars anteriorly and that the angle in the two groups is the same. The joints between the two hyoid rami allow only small and variable movements and the angle between the rami varies greatly among the different percoids. Furthermore, there are no morphological specializations in the joint between the interhyal and the suspensory apparatus that are adaptive to pressing each half of the suspensorium laterally. The joints at either end of the interhyal are simple cartilage joints allowing movements in many directions. It is unlikely that such highly flexible joints at the proximal and distal ends of the interhyal can act as major abductors of the suspensory apparatus. The epihyal has no special features for pushing the suspensory apparatus laterally against the resistance of the water. The smooth outer surface of the hyoid slides easily against and along the smooth inner surfaces of the suspensory apparatus and interopercular. All surfaces are covered by an epithelium, which is relatively rich in mucous glands. Since the force exerted by the hyoid is not perpendicular to the curved surfaces of the suspensory apparatus, considerable sliding between the opposing elements is inevitable. In experiment g the interhyals have been removed (Fig. 56). The effects of this surgical procedure on the pattern and degree of movements of the cranial elements are minimal. Abduction of the suspensory apparatus seems more pronounced in the absence of the interhyals (Fig. 56). This indicates that the interhyals do not play a role in abduction of the suspensory apparatus. In experiment h the connection between urohyal and hyoid has been interrupted. By this surgical procedure the function of the sternohyoideus muscle, which inserts on the urohyal, has been eliminated. As a consequence, the hyoid apparatus remains virtually stationary. However, abduction of the suspensory apparatus proceeds normally (Fig. 56). We have, therefore, both morpholotical and experimental evidence that the hyoid apparatus plays either no role or at the most a very minor role in abducting the suspensory apparatus.

Motion Analysis of Deglutition

The best analysis of deglutition in teleosts is that of vanden Berghe (1928), who has made observations on *Cottus bubalus* and *Blennius pholis.* Vanden Berghe's study was based on live specimens feeding on bulky and elongate food (annelids). Both *Cottus* and *Blennius* swallow prey by alternating protraction and retraction of the upper jaw followed by movements of the gill arches that result in posterior movements of the prey over distances of 7 to 10 mm. Vanden Berghe concluded that the retractor ossium pharyngealium muscles are mainly responsible for the final stages of deglutition and that the levators arcuum branchialium muscles are the principal protractors.

No observations have been made on deglutition in percoids. Most workers after vanden Berghe have made functional conclusions based on purely morphological data. Conclusions on function based on fixed material is often hazardous. Movements of bony elements studied on freshly-killed animals vary greatly both quantitatively and qualitatively. The direction of muscle fibers is often altered beyond recognition in fixed material. The nandids seem to represent an appropriate group for deglutition studies, since they are capable of swallowing very large prey.

1. METHODS

Large or elongate live prey was fed to *Polycentrus* and *Monocirrhus.* Deglutition was slow and lasted up to two hours. Motion pictures were made of selected sequences of swallowing (Fig. 60) and the film was subjected to frame-by-frame analysis. Scaleless albino *Clarias* sp. proved to be the best prey, since it was elongate, but bulky anteriorly and slender posteriorly (Fig. 62). The pelvic spines of *Clarias* should be removed before offering it as prey to *Monocirrhus. Monocirrhus* with a standard length of 6–8 cm. is capable of swallowing *Clarias* of the same length.

In order to study the role of the gill arches in swallowing, *Monocirrhus* was fed albino scaleless *Clarias.* After the prey was swallowed *in toto,* the predator was killed and the prey dissected out of the predator's stomach. The prey was then fixed in a solution of 25 parts phenol, 50 parts glycerine, five parts formaldehyde, five parts 95 per cent alcohol, and 15 parts water. This solution prevents shrinkage. Standard alcohol and formalin fixatives cause shrinkage to such an extent that toothmarks left on the scaleless albino skin of *Clarias* totally or partly disappear. The diluted standard embalming solution will fix the skin with minimal shrinkage. The toothmarks preserved in the skin furnish important data concerning the pharyngeal phase of deglutition (Figs. 61–63). Removal of the opercular is impractical in the study of movements of gill arches, since the red gills obscure the arches significantly. Cinefluorescent techniques are inadequate because most gill arches lack the necessary density for clear X-ray images and overlap of images represents a virtually insurmountable hindrance.

2. GENERAL REMARKS

Before analyzing the details of deglutition, some general observations are made to enhance the clarity of subsequent analysis. In all observed cases deglutition of large prey by nandids proceeds in three distinct phases or steps. In the first phase, *the gnathous phase of deglutition,* the prey is moved into the buccopharynx by action of the upper and lower jaws. Deglutition begins always with the gnathous phase, which lasts for less than half of the total time required for deglutition. The second phase, *the gnathopharyngeal phase of deglutition,* depends on the action of both the jaws and the gill arches, which move the prey further backward by complex co-ordinated movements. The relative duration of the gnathopharyngeal phase is directly proportional to the length of the prey. The third and final phase, *the pharyngeal phase of deglutition,* depends on the movements of various components of the gill arches. The pharyngeal phase is generally the shortest.

Deglutition is a continuous process and the proposed subdivision may seem somewhat arbitrary, however, the subdivision reflects the mutual dependency and independency of associated functional units. This analysis is mainly based on *Monocirrhus,* but comparative observations have been made on *Polycentrus schomburgkii* and *Nandus nebulosus.*

3. THE GNATHOUS PHASE OF DEGLUTITION

The first phase of deglutition is realized by action of the upper and lower jaws. Figure 60A and B represents two steps of the

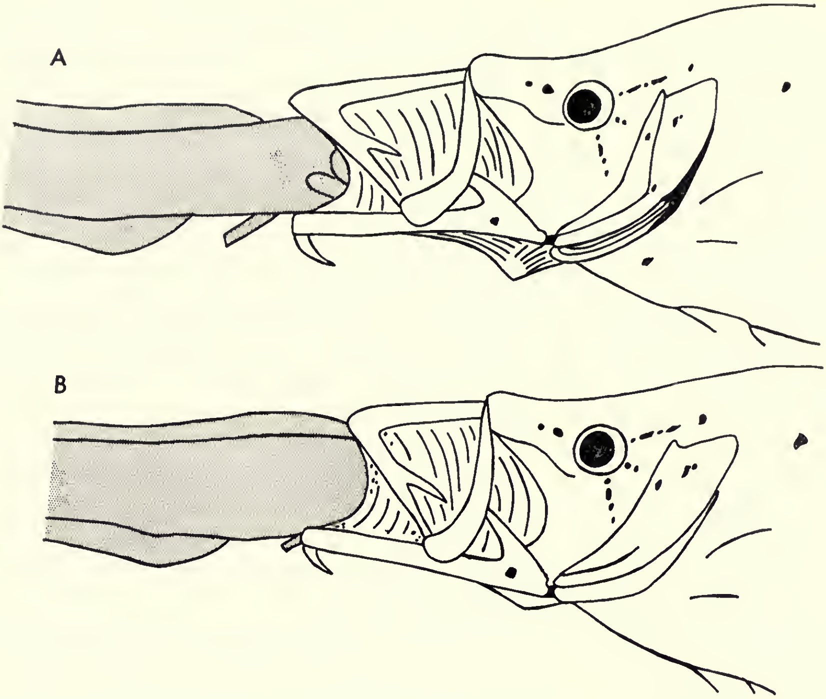

FIG. 60. Tracings of frames of motion pictures of *Monocirrhus polyacanthus* while swallowing scaleless, albino *Clarias* sp.

A. Initial capture of prey. Jaws are fully protruded and maxilla is rotated anteriorly into a somewhat oblique position. Urohyal is pulled posteroventrally. Suspensory apparatus is fully abducted.

B. After initial capture of prey, the jaws are retracted by pulling back the maxilla into a vertical position via the action of the adductor mandibulae muscle. Retraction of the jaws pulls the prey farther into the predator's buccopharynx. The distance of progress equals the distance between the initial bite and the anterior border of the dorsal fin (compare A and B). During retraction, the suspensory apparatus is partially abducted. The urohyal is pulled anterodorsally, but it is still visible anteroventral to the quadratomandibular joint.

gnathous phase. In Figure 60A the large prey has just been captured by extreme protrusion of both the upper and lower jaws. The maxilla is rotated as far forward as possible in an oblique position. The mandible is horizontal. The anterior tips of the mandible and premaxilla are in one vertical plane. The hyoid apparatus is depressed far ventrally and the opercular and suspensory apparatus are greatly abducted. The suspensory apparatus remains abducted throughout the process of deglutition. The jaws remain open and protruded as long as the prey is in the buccal cavity. During the

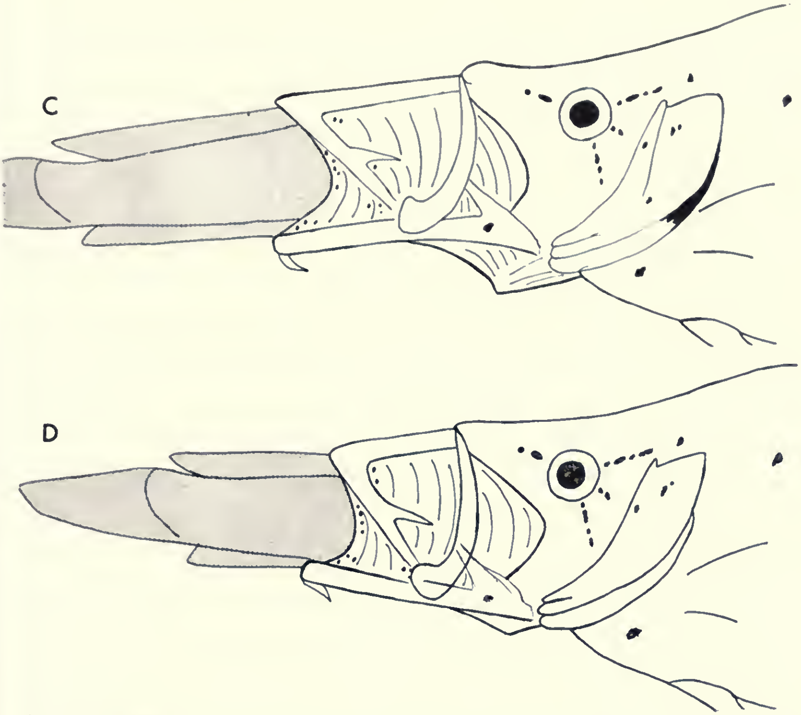

Fig. 60. *cont.*

C. After retraction, the jaws are protracted and are fixed at a more posterior position on the prey. The positions of the bones are identical to those in A.

D. Protraction is followed by retraction through the same mechanism as described in B. Protraction and retraction continue to alternate until completion of swallowing process.

gnathous phase of deglutition, both upper and lower jaws alternate protractory and retractory movements. The prey is captured by maximal protrusion of the jaws (Fig. 60A). In the next step, the premaxillae are retracted over a distance of one-sixth the length of the head or approximately 0.6 cm. in a specimen of 8 cm. in standard length. The prey is moved over the same distance, i.e., one-sixth the length of the head, into the buccopharynx of the predator. Retraction of the premaxillae is always accomplished by slight adduction of the mandible (Fig. 60B). The mandible is in a slightly oblique position. The maxilla is also retracted from its oblique position into a vertical position (Fig. 60B). Retraction of the premaxillae proceeds, while the mouth is fully open. During retraction of the premaxillae, the suspensory apparatus remains fully abducted, but the hyoid apparatus is partially retracted. Retraction of premaxillae with abducted suspensory apparatus seems impossible in other acanthopterygians (Alexander, 1967) and cyprinids (Alexander, 1966). After the prey has advanced into the predator's buccopharynx over the distance covered by the retracting premaxillae, the predator opens its mouth, disengages the teeth from the prey and swims forward by a quick and sudden jerk. Meanwhile, the jaws are protracted and placed further along the prey's body. The distances between successive bites are equal to the combined distances of successive protraction and retraction of the premaxillae. The impressions of the teeth of the jaws in the prey's skin (Figs. 61, 62, 63) are guidelines for the interpretation of deglutition. The two intervals between the first three bites are larger than the following ones (Fig. 61). The first three bites represent the gnathous phase. The anterior third of the prey is swallowed during the gnathous phase by the sole action of the jaws. After the third bite the pharyngeal mechanism is activated and the impression of the teeth of the jaws becomes much more frequent and the interval between successive bites much shorter (Figs. 61, 62, 63). The long interval between the first three bites and the fact that the distance between the anterior tip of the prey and the impression of the third bite equals the distance between the anterior tip of the prevomer and the anterior margin of the tooth-bearing pharyngeal bone can only be interpreted as evidence that the initial phase of deglutition proceeds by alternating protractory and retractory movements of the jaws. No other tooth-bearing structures are involved in this phase, and it is inconceivable that protraction of the hyoid apparatus will have any effect on swallowing prey of this nature.

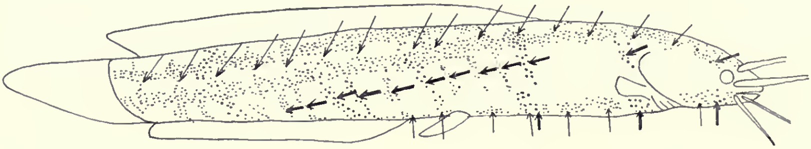

FIG. 61. Lateral aspect of scaleless albino *Clarias batrachus* (standard length 8.1 cm.) retrieved from stomach of *Monocirrhus* just after it was swallowed. Toothmarks on prey are impressions of the premaxillary teeth (heavy oblique arrows), mandibular teeth (heavy vertical arrows), upper pharyngeal teeth (light oblique arrows), and lower pharyngeal teeth (light vertical arrows). The arrows indicate successive "bites." Spacings between successive arrows represent the excursions of the respective teeth-bearing bones.

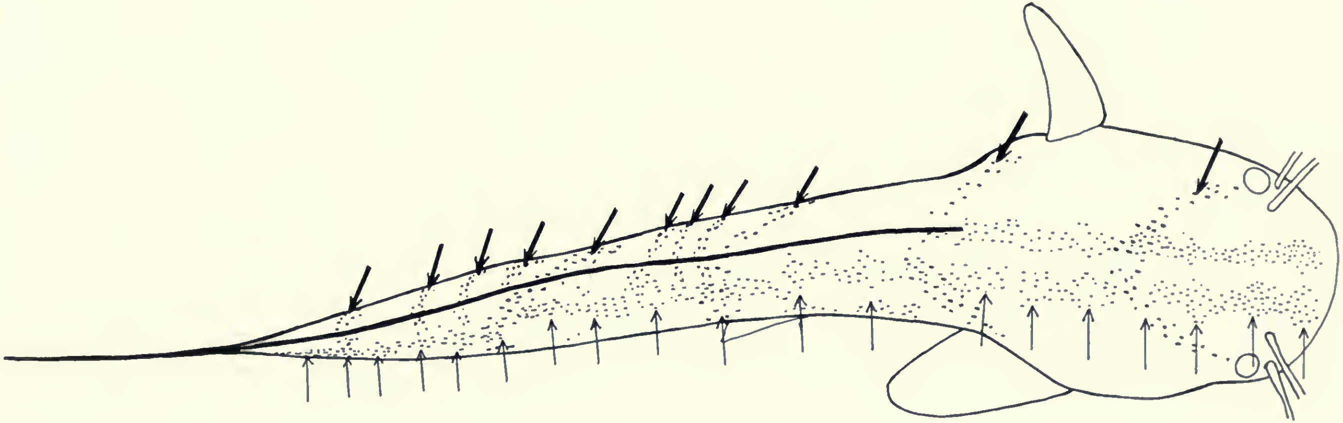

FIG. 62. Dorsal aspect of *Clarias batrachus* (same specimen as in Fig. 61). Toothmarks on prey are impressions of premaxillary teeth (heavy, oblique arrows) and upper pharyngeals (light, vertical arrows). Spacings in between successive heavy and light arrows represent excursions of, respectively, the premaxillae and upper pharyngeals.

4. THE GNATHOPHARYNGEAL PHASE OF DEGLUTITION

After the third bite, deglutition proceeds by action of both the jaw and branchial mechanisms. The frequency of bites is increased and synchronized with the frequency of impressions of the teeth of the upper and lower pharyngeal bones (Figs. 61, 62, 63). Deglutition during the gnathopharyngeal phase is slower than during the gnathous phase. The prey advances toward the gullet over distances that correspond to the length of the upper pharyngeal bones. The impressions of the teeth of the upper pharyngeal bones are continuous (Fig. 61). This indicates that the toothmarks of the anterior margin of the pharyngeal bones overlap with those of the anterior margin in the next bite. Therefore, the maximal excursion of the upper pharyngeal bones does not exceed the length of the bones. The prey progresses with every inspiratory movement. Each swallowing act during the gnathopharyngeal phase is accompanied by mouth opening, disengagement of the teeth of the jaws from the prey, extreme abduction of the suspensory apparatus, and posteroventral movement of the hyoid. The prey moves over a distance of about 3 mm. in each swallowing act. During the gnathopharyngeal phase the jaws seem to function to hold the prey, rather than to move the prey posteriorly. Excursion of the prey is realized by movements of the tooth-bearing upper and lower pharyngeal bones, because the distance of excursion of the prey corresponds with the length of the upper pharyngeal bones. Retraction by the pharyngeal apparatus takes place during inspiration only.

The tooth-bearing lower pharyngeal bones, i.e., the fifth ceratobranchials play an important role during the gnathopharyngeal phase of deglutition. The toothmarks on the ventral surface of the prey (Fig. 63) are distinctly interspaced indicating that the fifth ceratobranchials undergo protractory and retractory movements in co-ordination with similar motions of the upper pharyngeals. Vanden Berghe (1928) stated that in *Cottus* the fifth ceratobranchials do not move independently because they form an integral part of the branchial basket. The condition in nandids seems quite different, because regular interspacing of patches of toothmarks of the ceratobranchials on the ventral surface of the prey would not occur unless the ceratobranchials could move independently.

5. THE PHARYNGEAL PHASE OF DEGLUTITION

During the final stages of the gnathopharyngeal phase, the prey becomes twisted and is swallowed "sideways," i.e., the vertical plane

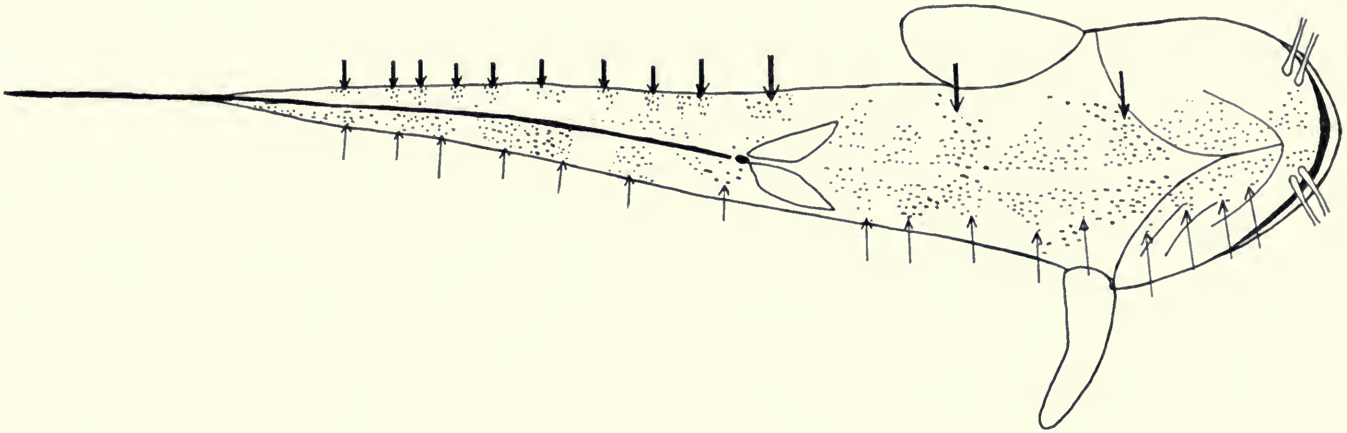

FIG. 63. Ventral aspect of *Clarias batrachus* (same specimen as in Fig. 61). Toothmarks on prey are impressions of mandibular teeth (heavy vertical arrows) and lower pharyngeal teeth (light vertical arrows). Spacings in between successive heavy and light arrows represent excursions of, respectively, the mandible and lower pharyngeals.

of the posterior half of the prey is rotated into a horizontal position. The pharyngeal phase of deglutition is involved in swallowing the last third of the prey. In Figures 61 and 63 one can see from the tooth patches that the right side of the posterior third of the prey bears the toothmarks of the upper pharyngeals and the left side exhibits the marks of the ceratobranchials. During the pharyngeal phase, the jaws are excluded from deglutition and the prey is no longer protruding from the predator's mouth. The jaws open and close rhythmically, while the suspensory apparatus remains partially abducted, although the degree of abduction varies rhythmically. The pharyngeal phase of deglutition is terminated when the suspensory apparatus is fully adducted. Deglutition during the pharyngeal phase proceeds by co-ordinated protractory and retractory movements of both the upper and lower teeth-bearing pharyngeals. Because there is no transition between gnathopharyngeal and pharyngeal phases in respect to pattern of toothmarks, we have to conclude that the jaws do not play a role in deglutition, except in the initial stages. The intervals between successive patches of toothmarks in the ventral surface of the posterior third of the prey are similar to those of the anterior two-thirds of the prey. This means that the prey advances toward the gullet at a uniform rate of speed. We may conclude that maximal excursion of the upper pharyngeals does not exceed their own length and that the lower pharyngeals move over a distance slightly more than their total length. Since there is no significant change in the speed by which the prey is swallowed, we have to conclude that the diameter of the prey has little influence on the degree of excursion of the pharyngeal bones. The diameter of the posterior third of the prey is significantly smaller than that of the more anterior regions (Fig. 62), yet the speed of swallowing remains constant during the two final phases. We may also postulate that the excursion of the pharyngeal bones as exhibited by toothmarks on this prey (Fig. 63) represents the maximal value.

Morphological Basis of Deglutition

Deglutition involves the neurocranium, the suspensory apparatus, jaws, hyoid, pectoral girdle, branchial basket, the vertebral column, and to a much lesser extent, the opercular apparatus. It is, therefore, conceivable that these units are mutually interdependent in the realization of the deglutitionary function. The nature of the interdependency is mainly mechanical, although structural and positional influences are undoubtedly present but difficult to prove.

1. FUNCTIONAL ANATOMY OF THE GNATHOUS PHASE

Protrusion and opening of the jaws proceed in the same manner as described under "Functional Morphological Analysis." However, once the prey has been captured, the swallowing mechanism is activated. During the gnathous phase, the jaws are protracted and retracted alternately. Partial retraction is caused by contraction of the adductor mandibulae muscles. Contraction of the adductor mandibulae muscles will cause tension in the tendon, which pulls the maxilla from the forward oblique position into a vertical position and the mandible from a horizontal to an oblique position (Figs. 60, A–D). The force of the adductor mandibulae acts just below the fixed position of the maxilla against the nasal (Figs. 33, 58). Since this force acts below the stationary maxillonasal joint, it will pull the maxilla posteriorly, i.e., retract it. Retraction of the maxilla will be transmitted to the ventral end of the premaxilla resulting in a retraction of the upper jaw. The action of the adductor mandibulae muscles can easily be interrupted by cutting the tendon (see experiment f under "Motion Analysis"). With the severed tendon of the adductor mandibulae muscles, the mouth remains partially open and protruded. No adduction occurs. *Monocirrhus* is able to retract its premaxillae while the suspensory apparatus is greatly abducted. Alexander (1967) has demonstrated that in generalized acanthopterygians the premaxillae cannot be retracted until the suspensory apparatus is adducted, because in the abducted state of the suspensoria, the maxillary processes of the palatines are pointed dorsomedially forming an effective hindrance to any retraction of the upper jaws. However, in *Monocirrhus* a large cartilaginous palatopterygoid joint enables the suspensory apparatus to move independently from the palatine (Figs. 16, 45). During extreme abduction of the suspensory apparatus a large angle is formed between palatine and the rest of the suspensory apparatus. Consequently, the maxillary processes of the palatine are not forced dorsomedially and retraction of the jaws is not hindered during swallowing while the suspensory apparatus is greatly abducted. The cartilaginous palatopterygoid joint may be regarded as a special adaptation to swallowing large prey during which retraction of the jaws with greatly abducted suspensoria is a prerequisite. The mechanical interdependence between the jaw and suspensory apparatus is clearly reflected in the mechanical dissociation of the palatine from the suspensorium.

Protractory movements of the jaws during swallowing are the result of the action of the sternohyoid-hyoid-interopercular-mandible coupling (see "Functional Morphological Analysis"). Protraction and opening of the jaws during deglutition is always preceded or accompanied by posteroventral movement of the hyoid apparatus (Fig. 60). No posterodorsal movement of the opercular can be seen during deglutition indicating that the levator operculi-opercular apparatus-mandible coupling does not participate significantly in the swallowing act. The differentiation of a strong and distinct interoperculo-hyoid ligament seems to be correlated with the specialized mechanisms to capture and swallow large prey. The efficiency of the sternohyoid-hyoid-interopercular-mandible coupling depends on two characteristics (van Dobben, 1937): (1) The length of the interhyal. The rod-like interhyal swings backward and forward from its dorsal attachment to the symplectic process of the hyomandibular. The longer the interhyal, the greater the excursion of the ventral end of the interhyal. The greater the excursion of the ventral end of the interhyal, the greater the excursion of the interopercular with which it is attached ligamentously. The larger the excursion of the interopercular, the more the mandible is depressed. (2) The vertical distance between the interoperculomandibular ligament and quadratomandibular joint. The shorter the distance, the better the transmission of the posterodorsally-directed force on the mandible. When the distance is short, a small excursion of the interopercular will depress the mandible over a large distance. Among nandids, *Polycentropsis* and *Monocirrhus* have the longest interhyals (Figs. 24, 25) and *Afronandus* the shortest, while those of *Polycentrus* and *Nandus* are of intermediate lengths. The extraordinary length of the interhyal seems to be correlated with obtaining an increased efficiency of the sternohyoid-hyoid-interopercular-mandible coupling, which controls the important final stages of extreme jaw protrusion and the protractory movements of the jaws during the gnathous phase of deglutition of large prey *in toto.* The vertical distance between interoperculo-mandibular ligament and quadratomandibular joint is shortest in *Monocirrhus* and *Polycentropsis.* However, since the force exerted on the mandible has shifted from a purely posterior and horizontal direction to a more dorsal and vertical direction in nandids, the elongate posteroventral portion of the mandible will increase the moment arm of the force in the interoperculomandibular ligament. The increased moment arm will enhance the effectiveness of the sternohyoid-hyoid-interopercular-mandible coupling. The moment arm is the longest in *Monocirrhus* and *Polycentropsis* and the shortest in *Afronandus.*

2. FUNCTIONAL ANATOMY OF THE GNATHOPHARYNGEAL AND PHARYNGEAL PHASE

The major function of the jaws during the gnathopharyngeal phase is to hold the struggling prey. The pattern and speed of deglutition do not change during the transition from gnathopharyngeal to pharyngeal phase, indicating that the pharyngeal apparatus is solely responsible for deglutition of the last two-thirds of the prey, with the jaws performing only a secondary holding role. The jaws are operated by the sternohyoid-hyoid-interopercular-mandible coupling as described in the previous chapter.

The mechanical units involved in the gnathopharyngeal and pharyngeal phases of deglutition are the neurocranium, the anterior vertebral column, the pectoral girdle, the hyoid apparatus, the jaws, and the branchial basket (Fig. 64). Complex mechanical interactions take place between these units in realizing the swallowing mechanism. The pharyngeal mechanism depends mainly on movements of the tooth-bearing upper and lower pharyngeals and the hyoid apparatus (Fig. 65). The neurocranium, vertebral column, and pectoral girdle are relatively stationary. Deglutition is caused directly by movements of the upper and lower pharyngeals (Fig. 65).

a. The upper pharyngeals

The upper pharyngeal undergoes protractory and retractory movements accompanied, respectively, by a turning of the anterior

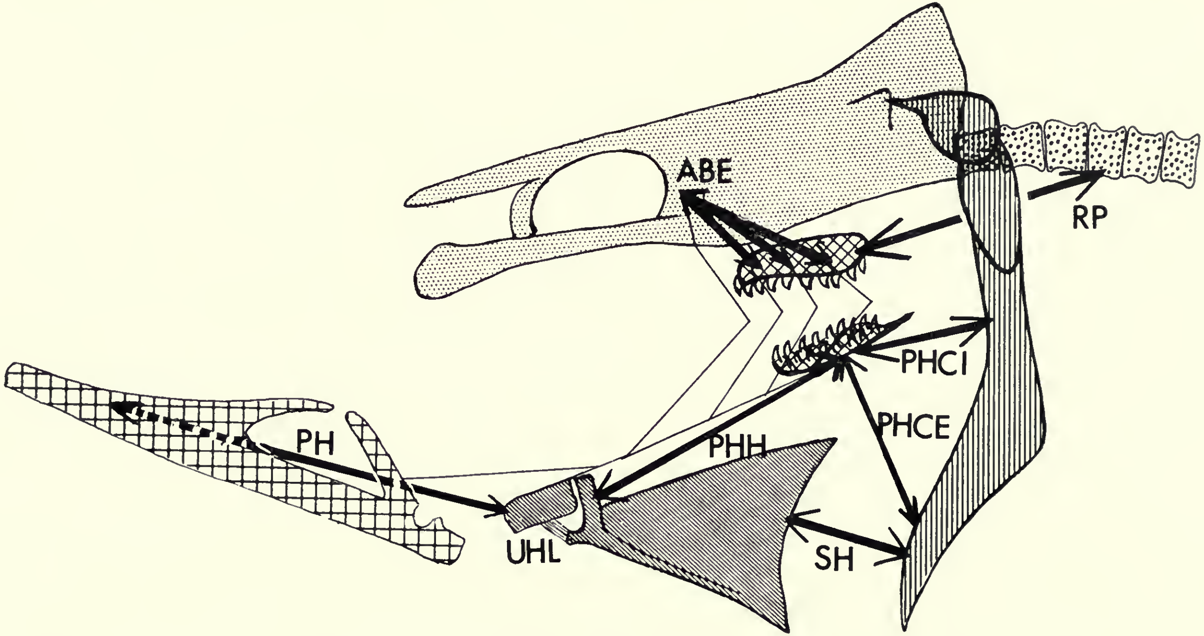

FIG. 64. Lateral aspects of principle units involved in the gnathopharyngeal phases of deglutition. Arrows indicate fiber or tendon direction of muscles. Branchial basket has been faintly indicated by light lines. Finely stippled area is neurocranium; heavily dotted area is vertebral column; obliquely cross-hatched areas are upper and lower pharyngeals of branchial apparatus; obliquely and finely lined area is urohyal and hypohyal; vertically and heavily lined area is pectoral girdle; perpendicularly cross-hatched area is mandible. ABE, levator arcuum branchialium externi; PH, protractor hyoideus; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PHH, pharyngohyoideus; RP, retractor ossium pharyngealium; SH, sternohyoideus; UHL, urohyalohypohyal.

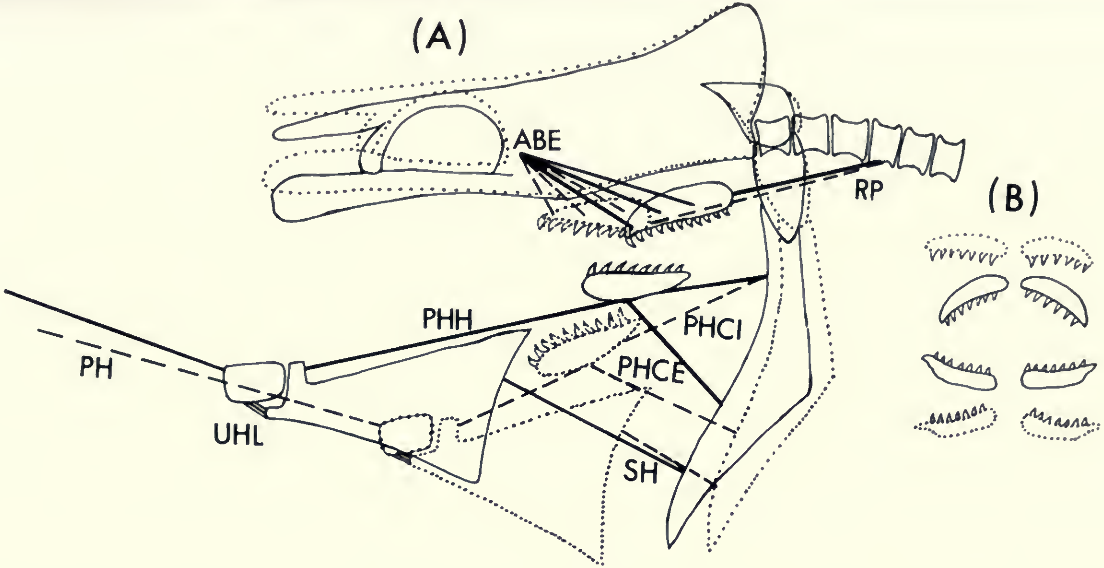

FIG. 65. A, Simplified diagram depicting movements of pharyngeal bones and urohyal from a lateral aspect. Broken lines indicate position and condition of muscles during protraction of the pharyngeals. Solid lines depict position and condition of muscles during retraction of the pharyngeals. Bony elements in solid lines represent positions during full retraction, while dotted outlines indicate positions of bones during extreme protraction. During deglutition, protraction and retraction occur in an alternating pattern. B, Frontal aspect of upper and lower pharyngeals. Solid line depicts positions during retraction, dotted line represents positions during protraction. ABE, levator arcuum branchialium externus; PH, protractor hyoideus; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PHH, pharyngohyoideus; RP, retractor ossium pharyngealium; SH, sternohyoideus; UHL, urohyalohypohyal ligament.

tip dorsally and a rotation of the posterior tip ventrally. Rotation of the anterior tip dorsally during protraction will bring the curved teeth into a progressively more posterior location of the prey. The pharyngeal teeth are strictly prehensile. During retraction the anterior tip rotates posteroventrally, moving the prey toward the esophagus. No articulation between the upper pharyngeals and neurocranium exists. During protraction the upper pharyngeals are abducted, i.e., the lateral border moves dorsolaterally (Fig. 65). Abduction of the upper pharyngeal will disengage the teeth from the prey. Retraction is always accompanied by a marked adduction of the upper pharyngeals, i.e., the lateral borders move ventromedially, resulting in a continuous firm grip on the prey by the teeth.

Retraction is caused by contraction of the elongate, parallel-fibered retractor ossium pharyngealium muscles (Figs. 38, 39, 64, 65). Because of the divergence from origin to insertion of the two muscles, contraction will not only retract, but will also cause a convergent movement, i.e., slight adduction, of the upper pharyngeals. The upper pharyngeals move over a distance slightly less than half of the resting length of the retractor ossium pharyngealium muscles. The excursion of the upper pharyngeals can be measured from the toothmarks on the prey (Fig. 61). The resting length of the muscles can be estimated in anesthetized predators. The distance of excursion of the upper pharyngeals is directly proportional to the length of the retractor ossium pharyngealium muscles. The distance of excursion of the upper pharyngeal never exceeds half the resting length of the muscles.

Protraction of the upper pharyngeals is caused by contraction of the levator arcuum branchialium externi muscles. The name, levator, is quite misleading. This series of muscles has been described from fixed specimens (Vetter, 1874; Dietz, 1914) in which the true functions were not immediately recognized. The topography of these muscles in living condition is very different from that in fixed specimens. The levator arcuum branchialium externi muscles in resting condition in anesthetized fish run in an anteroposterior direction, rather than dorsoventral. Vanden Berghe (1928) stimulated the levator arcuum branchialium externi muscles in live *Cottus* and *Blennius* electrically, causing protraction of the upper pharyngeals. In *Monocirrhus* the levator arcuum branchialium externi muscles are the principal protractors of the upper pharyngeals. The protractory excursion of the upper pharyngeal corresponds to one-third the resting length of the levator arcuum branchialium externi muscles. The angulation of the muscle fibers on the upper pharyngeals becomes gradually more acute as protraction progresses (Fig. 65). Toward the end of protraction the levator arcuum branchialium externi muscles will lift the anterior end of the upper pharyngeal dorsally, while abducting the bone.

Adduction of the upper pharyngeals is caused by contraction of the transversus dorsalis muscles and the retractor ossium pharyngealium muscles during the retractory cycle. Abduction of the upper pharyngeals is accomplished during protraction by the obliquus dorsalis, levator arcuum branchialium interni, and to a lesser extent, externi muscles.

b. The lower pharyngeals

The fifth ceratobranchials bear teeth and are referred to as lower pharyngeals. The lower pharyngeals undergo protractory, retractory, adductory, and abductory motions (Fig. 65). The toothmarks on the prey furnish important data on the degree, rhythm, and nature of the movements of the lower pharyngeals (Figs. 62, 63). Muscles directly involved in the operation of the lower pharyngeals are the pharyngocleithralis internus and externus and the pharyngohyoideus. Indirectly, the sternohyoideus and protractor hyoideus muscles play a major role in the operation of the lower pharyngeals and the branchial apparatus as a whole. For clarity the direct muscular influences on the lower pharyngeals will be considered first and separately. Functional analysis of the branchial basket as a whole is discussed at the end of this chapter.

Most authors have elaborated on the role of the upper pharyngeals during deglutition (Vanden Berghe, 1928; Tchernavin, 1948; Waterman, 1948; Tchernavin, 1953; Günther and Deckert, 1955). Vanden Berghe (1928) has stated that the lower pharyngeals do not move independently from the branchial basket. Kayser (1962) and Karrer (1967) have suggested that the lower pharyngeals move forward and backward as a result of alternating contractions of, respectively, the protractor hyoideus and sternohyoideus muscles. The role of the lower pharyngeals during deglutition has escaped the attention of most authors. The toothmarks on the prey (Figs. 61, 63) clearly indicate that the lower pharyngeals can move freely. The impressions of the teeth of the ceratobranchials form distinctly patterned patches with regular interspaces between successive "bites." Were the ceratobranchials unable to move independently, the toothmarks would not form distinctly patterned and interspaced patches, but, instead, longitudinal continuous or irregularly interrupted bands.

Protraction of the lower pharyngeal is caused by the pharyngohyoideus muscle, which draws the lower pharyngeal anteriad and ventrad toward the urohyal, while the hyoid is moving posteroventrally by simultaneous contraction of the sternohyoideus muscle (Fig. 65). The pharyngocleithralis externus muscle also aids in protraction by pulling the lower pharyngeal ventrad.

Abduction of the lower pharyngeal accompanies protraction and is caused by contraction of the pharyngocleithralis externus muscle (Fig. 65, A and B). During protraction and abduction of the lower pharyngeals the pharyngocleithralis internus and protractor hyoideus muscles are relaxed and stretched.

Retraction of the lower pharyngeal is caused by the pharyngocleithralis internus, which is the chief antagonist of the pharyngohyoideus muscle. Contraction of the pharyngocleithralis internus muscle will pull the lower pharyngeal posteriad and dorsad. During retraction of the lower pharyngeal, the pharyngocleithralis externus, sternohyoideus, and pharyngohyoideus are relaxed, allowing the lower pharyngeal relatively independent movement posteriorly and dorsally. The protractor hyoideus muscle contracts just prior to contraction of the pharyngocleithralis internus, pulling the urohyal anteriad and dorsad.

Adduction of the lower pharyngeals accompanies retraction. The chief adductors of the lower pharyngeals are the transversus ventralis muscles.

c. The branchial apparatus as a whole

Karrer (1967) has suggested that the movements of the upper and lower pharyngeals are co-ordinated in such a way that when the upper pharyngeals are protracted the lower are retracted. Protraction and retraction of the upper and lower pharyngeals would, therefore, alternate. The toothmarks on the prey cannot either disprove or prove the existence of such a co-ordination. However, functionally, there is no evidence for the hypothesis that retraction of the upper pharyngeal is synchronized with protraction of the fifth ceratobranchials in *Monocirrhus*. Protraction of the upper pharyngeals accompanied by retraction of the lowers will not enhance deglutition of large prey. Protraction of upper pharyngeals occurs to disengage the teeth from the original site of the "bite" and to fix the teeth in a new, more posterior position of the prey. This activity will be difficult or impossible if the large prey is pressed dorsally against the upper pharyngeals by the retracting lower pharyngeals (Fig. 65). Simultaneous protraction of the upper and lower pharyngeals will insure maximal distance between the two tooth-bearing elements allowing easy disengagement of the teeth from the prey. After disengagement of the teeth from the original "bite," refixing at a new and more posterior location of the prey can occur (Fig. 61). Retraction of the upper pharyngeals accompanied by protraction of the lower pharyngeals will not decrease the distance between the tooth-bearing elements resulting in a decrease of the intensity of the grip of the teeth on struggling prey. Furthermore, the force exerted on the prey will be limited to the ventral surface only. On the other hand, simultaneous retraction of the upper and lower pharyngeals, has two functional advantages: (1) both tooth-bearing elements remain adducted so that the firm grip on the prey is not lost; (2) retractory forces will work simultaneously on the dorsal and ventral surfaces of the prey. There is strong morphological evidence in favor of the simultaneous protraction and retraction of upper and lower pharyngeals hypothesis over that of the alternating hypothesis proposed by Karrer (1967). The upper and lower pharyngeals are closely integrated with the other elements of the branchial apparatus by ligaments, joints, and muscles (Günther and Deckert, 1953, 1955; Kampf, 1961; Kayser, 1962). In all nandids the hypohyalobasibranchial ligament extends between the dorsomedial margin of the posteromedial corner of the dorsal hypohyal and the anterolateral surface of the first basibranchial. Any movement of the hyoid, caused by contraction of either the protractor hyoideus or sternohyoideus will be transmitted to the branchial basket (Fig. 65). The short, but strong, urohyalohypohyal ligament runs between the anterior process of the urohyal and the posteroventral surface of the hypohyal. This ligament transmits any movement of the urohyal to the hyoid bars. We can, therefore, recognize the *sternohyoideus-hyoid-branchial apparatus-protractor hyoideus coupling*, which transmits the posteroventral and anterodorsal movements of the hyoid apparatus directly to the branchial basket. However, the upper and lower pharyngeals are operated by two separate couplings that work in close co-operation with the sternohyoideus-hyoid-branchial apparatus-protractor hyoideus coupling. The upper pharyngeals are associated with the *vertebral column-retractor pharyngealium-upper pharyngeal-levator branchialium-neurocranium coupling*, which protracts and retracts the upper pharyngeals. The lower pharyngeals are operated by the *pectoral girdle-pharyngocleithralis-lower pharyngeal-pharyngohyoideus-urohyal coupling*, which protracts and retracts the fifth ceratobranchials (Fig. 64).

It is remarkable that the branchial apparatus of nandids lacks the adductor arcuum branchialis muscles. Retraction of the branchial apparatus by the retractor ossium pharyngealium and the pharyngocleithralis internus muscle is accompanied by protraction of the urohyal by the protractor hyoideus muscle (Fig. 64). Retraction of the upper and lower pharyngeals reduces the vertical distance between the two bones (Fig. 65), causing the angle between ceratobranchial and epibranchial to become more acute, i.e., adduction. Retraction of the upper pharyngeals during deglutition coincides with the expiratory phase of the respiratory cycle during which water is forced, by compression of the buccopharyngeal cavity, across the gills into the opercular cavity (Hughes and Shelton, 1958; Liem, 1967c). Adduction of the branchial apparatus at the epibranchial-ceratobranchial joints occurs passively and indirectly by the activity of three retractory mechanisms.

The histology of the epibranchial-ceratobranchial joints in *Monocirrhus* corresponds with that of *Sparus* as described by Haines (1934). No muscles are associated with the joint (Fig. 66). There is neither a typical articular cartilage nor a joint cavity. Movement is allowed by the connective tissue between the two bones. Haines (1934) has ascribed two functions to the massive cartilaginous epiphysis of this type of joint: (1) ontogenetically, it provides unlimited longitudinal growth of the bone; (2) mechanically, it forms a resilient bearing surface, minimizing any sudden shock to the bony system, and at the same time allowing movements between the two bones. It is clear from Figure 66 that the two functions suggested by Haines also apply to the nandids, and perhaps, to all teleosts. The shape of the distal surfaces of the epiphyses and the limited amount of loose connective tissue at the obtuse angle of the joint suggest that there is a resistance to abduction of the joint (Fig. 66). It seems possible that adduction occurs automatically because of the morphology of the joints between the ceratobranchials and epibranchials. Indirect adduction by the retractory mechanisms may be aided by direct adduction because of intrinsic forces within the joint.

Abduction of the epibranchial-ceratobranchial joints is caused by indirect forces only. Protraction of the branchial apparatus by the levator arcuum branchialium externus and the pharyngohyoideus muscles accompanied by posteroventral displacement of the urohyal by contraction of the sternohyoideus, will increase the vertical distance between the upper and lower pharyngeals, causing the angles between the ceratobranchials and epibranchials to become less acute,

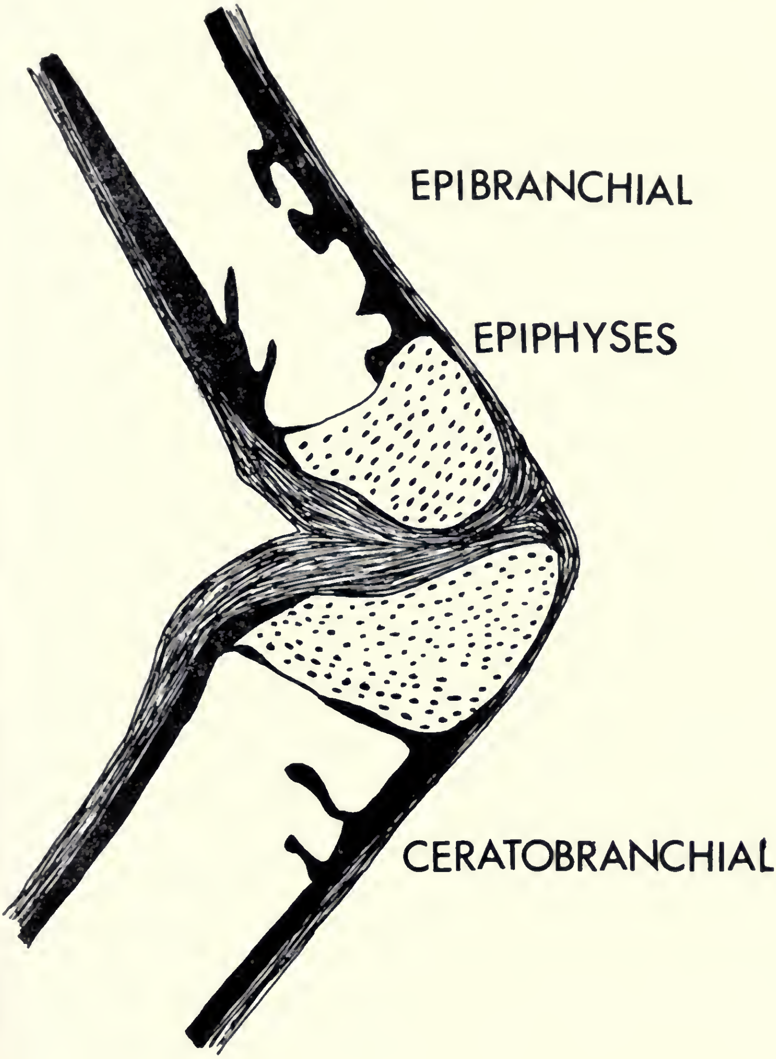

FIG. 66. Longitudinal section of the joint between first epibranchial and ceratobranchial of *Monocirrhus polyacanthus*. Bone is shown black, hyaline cartilage white, connective tissue as lines, and dots represent nuclei.

i.e., abduction (Fig. 65). Abduction of the ceratobranchial-epibranchial joints during deglutition coincides with the inspiratory phase of the respiratory cycle during which the buccopharyngeal cavity expands to suck water in.

Discussion

This final synthesis deals with: (1) the definition and generalization of adaptations to swallowing large prey *in toto* for percoid fishes; (2) the interdependency of structural elements within mechanical units and couplings during nandid evolution; (3) the mutual influences between respiratory and feeding mechanisms; (4) the phylogeny of nandids and the underlying evolutionary factors. The subdivision of this chapter into four separate entities is done for clarity. All four subchapters deal with the basic synthetic theme of evolutionary morphology which may eventually shed some light on the evolutionary molding factors underlying percoid radiation. Some of the generalizations will, undoubtedly, prove to be invalid, as more detailed functional anatomical studies become available.

1. ADAPTATIONS TO SWALLOWING LARGE PREY *IN TOTO*

The nandid genera *Monocirrhus* and *Polycentropsis* are highly specialized predators feeding exclusively on other fishes of considerable size. *Nandus* and *Afronandus* are also predators, but, in general, they do not swallow large prey *in toto* and their carnivorous diet is not restricted to fishes. *Polycentrus* is an intermediate, feeding on smaller fish and miscellaneous worms and arthropods (Barlow, 1967b).

Monocirrhus and *Polycentropsis* exhibit many highly specialized features specifically adaptive to swallowing large prey *in toto*. However, the specializations are very different from those of other fishes with a comparable size range of prey, e.g., *Chauliodus* (Tchernavin, 1953), *Gonostoma*, and *Cyclothone* (Günther and Deckert, 1955).

Polycentropsis and *Monocirrhus* have extremely large jaws (Figs. 15, 16, 20, 21). The position of the quadratomandibular joint has shifted posteroventrally (compare Figs. 20, 21 with 17, 18, 19). The extraordinary length of the ascending process of the premaxillae and that of the mandible is a primary adaptation to exceptional protrusibility of the jaws (compare Fig. 46 with 47 and 48), which enhance the grasping range and speed of the predator.

The skull of *Polycentropsis* and *Monocirrhus* is much deeper than that of other nandids. The increase in depth of the skull is the result of changes in the suspensory apparatus, while the neurocranium remains unchanged (Figs. 4–8). The increase in depth of the suspensory apparatus of *Polycentropsis* and *Monocirrhus* is due to the short horizontal limb of the preopercular (compare Figs. 20, 21 with 17) and the rotation of the long axis of the quadrate from a horizontal to a vertical position. The greater depth of the suspensory apparatus increases the volume of the oro-pharynx to accommodate and manipulate large prey and to enhance the buccopharyngeal pressure pump during respiration.

Jaw protrusion is caused by depression of the mandible. Even the "screw mechanism of the maxilla" as recognized by Alexander (1967) finds its driving force in the depression of the mandible. Surgical removal of the medial and anterior maxillomandibular ligaments will interrupt the transmission of mandibular movement to the maxilla and premaxilla abolishing upper jaw protrusion (see "Motion Analysis," experiment e). The high ascending process (coronoid process) of the dentary functions to reduce the slack in the maxillomandibular ligaments by creating a shorter bridge between upper jaw and mandible. All predaceous percoids possess high ascending processes of the dentary to increase the grasping speed. The high ascending processes of the dentary in percoids have no muscle insertions (Figs. 31, 33, 44) and play no role in increasing the torque around the quadratomandibular joint as previously postulated (e.g., Schaeffer and Rosen, 1961; Matthes, 1963; Liem, 1967a).

The large elongate jaws, the increased depth of the quadratomandibular joint, and the high ascending processes of the dentary increase the grasping range of the bite and enlarge the buccopharyngeal cavity to accommodate and manipulate large prey *in toto*.

In all nandids the subopercular is eliminated from the levator operculi-opercular apparatus-mandible coupling. The mandible and opercular are interconnected by the interopercular without mediation by the subopercular (Fig. 58). The elimination of one bone in this chain enhances the transmission of the movements of the opercular to the mandible. The efficiency of the transmission is the highest in *Polycentropsis* and *Monocirrhus* in which the interoperculomandibular and interoperculo-opercular ligaments lie in the same vertical line with the resultant force of the levator operculi muscle (Fig. 34: LIM, IOPL, LO; Fig. 58). In *Nandus, Afronandus,* and *Polycentrus* the interoperculomandibular ligament is horizontal and forms an angle with the interoperculo-opercular ligament (Figs. 29, 32). Because of this angle, the force transmitted from the opercular to the mandible has to be resolved into two components of which one will be virtually lost. This loss of force is minimized in *Polycentropsis* and *Monocirrhus* by positioning the two ligaments in one direct line with the resultant force of the levator operculi muscle.

The elimination of the subopercular from the levator operculi-opercular apparatus-mandible coupling and the positioning of the interoperculomandibular and interoperculo-opercular ligaments in one vertical line with the resultant force of the levator operculi greatly increase the speed and efficiency of opening and protrusion of the jaws and is regarded as specifically adaptive to predatory feeding habits.

The efficiency of the sternohyoid-hyoid-interopercular-mandible coupling is enhanced by the extraordinary length of the interhyal in *Polycentropsis* and *Monocirrhus* (Figs. 24, 25). The rod-like interhyal swings backward and forward from its dorsal attachment to the symplectic process of the hyomandibular. The longer the interhyal the greater the excursion of the ventral end, which is connected to the hyoid apparatus. The greater the movement of the hyoid the greater the excursion of the interopercular because of the interoperculohyoid ligament (Fig. 36). The degree of depression of the mandible is directly proportional to the degree of movement of the interopercular. The long interhyals are, therefore, specifically adaptive in predation by speeding and enhancing the final phases of jaw protrusion and opening by way of the sternohyoid-hyoid-interopercular-mandible coupling.

Swallowing very large prey *in toto* is restricted to *Monocirrhus* and *Polycentropsis* which have special modifications in the swallowing mechanisms, especially in connection with the gnathous phase of deglutition. *Monocirrhus* and *Polycentropsis* can retract their premaxillae while the suspensory apparatus is greatly abducted. In most percoids the premaxillae cannot be retracted until the suspensory apparatus is adducted, because abduction of the suspensory will rotate the maxillary processes of the palatines dorsomedially, preventing the ascending processes of the premaxillae from sliding backward (Alexander, 1967). In *Monocirrhus,* and to a lesser degree in *Polycentropsis,* the movements of the suspensory apparatus have become independent from the palatine by the incorporation of a large flexible cartilaginous palatopterygoid joint (Figs. 16, 45). Consequently, abduction of the suspensory apparatus results in an angle between the palatine and the pterygoid plate leaving the former free to move with the jaw apparatus. Rotation of the maxillary processes of the palatines does not occur during abduction of the suspensoria and ascending processes of the premaxillae can be retracted. In *Polycentropsis* the joint between ectopterygoid and palatine is mobile (Fig. 15: ECT, P), although the amount of cartilage is much less than in *Monocirrhus*. In *Nandus* and *Afronandus* the palatine is strongly connected to both ectopterygoid and entopterygoid (Figs. 12, 13). *Polycentrus* (Fig. 14) represents an intermediate condition in which the connection with the entopterygoid is virtually lost (Fig. 14).

Retraction of the premaxillae, while the suspensoria are greatly abducted, is a mechanical prerequisite for swallowing large prey *in toto* during the gnathous phase of the deglutition and is realized in *Monocirrhus* and *Polycentropsis* by a flexible joint between pterygoid plate and palatine.

The role of teeth in swallowing large prey *in toto* is well exhibited in *Monocirrhus*. There is a marked reduction in tooth-bearing elements. The teeth on the prevomer, parasphenoid, palatine, ectopterygoid, basihyal, and third hypobranchial, all present in *Nandus* (Figs. 4, 12, 22), are lost in *Monocirrhus*. All nandid teeth are slightly curved and conical and have holding, rather than penetrating, functions. Disengagement of teeth after each bite is a prerequisite for deglutition of large prey *in toto*. The dentition in *Monocirrhus* is restricted to the premaxillae, mandible, and the upper and lower pharyngeal bones, all of which are highly mobile bones undergoing protraction, retraction, adduction, abduction. Teeth on less mobile bones such as the prevomer, parasphenoid, palatine, and ectopterygoid hinder deglutition of large prey, since disengagement of the teeth will not readily occur.

The reduction of tooth-bearing elements and the restricted occurrence of small holding teeth on just those mobile bones that undergo protraction, retraction, abduction, and adduction are adaptive features to swallowing large prey *in toto*.

Protraction and retraction of the toothed fifth ceratobranchials are important during deglutition of large prey *in toto*. Protraction of the fifth ceratobranchials is accomplished by contraction of the sternohyoideus and pharyngohyoideus muscles (Fig. 65). During protraction the teeth disengage from the original bite and the toothed bone is brought forward and downward to be refixed at a more posterior location of the prey. The greater the distance of protraction the more efficient the deglutitionary mechanism. In *Monocirrhus* (Fig.

38) the pharyngohyoideus is not only very long, but also large. Enlargement of the muscle is made possible by the increased height of the dorsal process of the urohyal (Figs. 24, 25), which furnishes additional sites for muscle attachments. In fishes with more restricted movements of the toothed fifth ceratobranchials, the dorsal process of the urohyal is very low, e.g., *Nandus* (Fig. 22).

Contrary to the condition in *Chauliodus* (Tchernavin, 1953) and (Gunther and Deckert, 1955) the cleithra of *Monocirrhus* and *Polycentropsis* are virtually immobile. The movements of the cleithra could not be detected with the techniques used in this study.

2. INTERDEPENDENCY OF STRUCTURAL ELEMENTS WITHIN MECHANICAL UNITS AND COUPLINGS

Structural elements will influence each other in various ways (Dullemeijer, 1958). In this synthesis mechanical factors are emphasized. In general, the sense organs do not have a profound influence on the architecture of the nandid skull. *Polycentropsis* (Fig. 20) has extremely large eyes, whereas *Monocirrhus* possesses the smallest orbits among nandids (Fig. 21). Yet, the two genera resemble each other more closely than any other nandid genus in respect to neurocranium, suspensory apparatus, opercular apparatus, and cranial musculature (Figs. 7, 8, 20, 21). The great difference in eye size between the two genera has not led to any major structural differences in the surrounding regions of the skull. The great resemblance between the African *Polycentropsis* and South American *Monocirrhus* is directly correlated with the similarities in feeding mechanisms.

a. Neurocranium and associated couplings

The neurocranium is the most uniform mechanical unit in nandids. Intergeneric differences are minor. *Polycentropsis* and *Monocirrhus* have an elongate preorbital region involving the nasals, prevomer, ethmoid bones (Figs. 1–8). Pronounced elongation of the entire preorbital region of the skull often accompanies predaceous feeding mechanisms (Liem, 1967a). The elongate preorbital region of the neurocranium has evolved to accommodate the elongate jaw apparatus. There is an intimate mechanical and positional interaction between the long ascending processes of the premaxillae and the neurocranium (Eaton, 1935, 1943; Hofer, 1938; Liem, 1967a).

Other influencing units on the neurocranium are the vertebral column and branchial apparatus. The angle in the parasphenoid in *Monocirrhus* and *Polycentropsis* (Figs. 6, 7) is pronounced. This basicranial angle provides more space during deglutition of large prey *in toto* and a more "strategic" structural inter-relationship between upper pharyngeal bone, vertebral column, retractor arcuum pharyngealium, and levator arcuum branchialium muscles (Fig. 64). It is plainly evident from Figure 64 that the proper angulation of the parasphenoid and the corresponding curvature of the vertebral column are of great mechanical meaning in respect to degree of movement of the upper pharyngeal bone, the angle of muscle attachments of the retractor ossium pharyngealium and levator arcuum branchialium muscles.

b. Suspensory apparatus and associated couplings

The suspensory apparatus exhibits considerable variation in nandid evolution reflecting the multiple influences of surrounding units. In the series *Nandus, Afronandus, Polycentrus, Polycentropsis,* and *Monocirrhus* there is a progressive and cumulative trend toward the separation of the palatine from the suspensory apparatus (Figs. 12–16). In *Polycentropsis* the joint between palatine and ectopterygoid is mobile, making the former bone independent from the suspensory apparatus, which is a specific adaptation to swallowing large prey *in toto*. This trend culminated in the incorporation of the palatine into the jaw apparatus in *Monocirrhus* (Fig. 58), so that the bone can move freely with the jaws and independently from the suspensory apparatus. This morphological reorganization makes it mechanically possible for *Monocirrhus* to retract its jaws with abducted suspensoria, which is a prerequisite in deglutition of large prey *in toto*. The incorporation of the palatine into the jaw apparatus in *Monocirrhus* (the same condition is only foreshadowed in *Polycentropsis*) furnishes an example of how and why an element in a mechanical unit can dissociate and be reorganized in the course of evolution. In the Siganidae (Starks, 1907) and the Tetraodontoidei (Sarkar, 1960), respectively, part and the whole palatine became separated from the suspensory apparatus and incorporated with the neurocranium to function with the jaw apparatus.

The mechanical interdependency between the suspensory apparatus and the levator operculi-opercular apparatus-mandible coupling is reflected in the straight and vertical preopercular. The vertical position of the interopercular and the direct alignment of the interopercular ligaments with the resultant force of the levator operculi muscle greatly increase the efficiency of the levator operculi-opercular apparatus-mandible coupling. The vertical positioning of this coupling can be realized or accommodated only by concomitant increase in depth of the suspensory apparatus by an augmented vertical growth of the preopercular and the rotation of the quadrate from a horizontal to a vertical position. The reorganization of the levator operculi-opercular apparatus-mandible coupling from a horizontal to a vertical position has influenced the morphology of both the opercular apparatus and neurocranium in functional and spacial respects. It is impossible to postulate whether the progressively more vertical positioning of the levator operculi-opercular apparatus-mandible coupling is a primary evolutionary trend in nandids (Figs. 29, 32, 33). The concomitant changes in the suspensory apparatus are also intimately integrated with the feeding apparatus and cannot be considered secondary.

c. Jaw apparatus and associated couplings

The changes within the jaw apparatus are restricted to a progressive increase in length of all elements and ascending processes. The mutual influences between the jaw apparatus, the palatine, and neurocranium have been discussed above.

The progressive elongation of the mandible is accompanied by a gradual posteroventral shift of the quadratomandibular joint (Figs. 17–21), which is a rather common phenomenon among teleosts (Günther and Deckert, 1960). The positional shift of the joint is instrumental in the mechanical realization of the vertically reorganized levator operculi-opercular apparatus-mandible coupling, which has, in turn, a profound influence on the jaw apparatus (as discussed under b). The elongate jaws have, therefore, influenced the morphology of the suspensory apparatus and indirectly the opercular apparatus by determining the position of the quadratomandibular joint.

d. Opercular apparatus and associated couplings

The mechanical and positional inter-relationships between the opercular, jaw, and suspensory apparatus have been discussed above in respect to the interopercular. The changes within the opercular apparatus are progressive and cumulative in the series *Nandus*, *Afronandus*, *Polycentrus*, *Polycentropsis*, and *Monocirrhus*, and involve a reduction in size of the subopercular (Figs. 16–21). The relative size and position of the opercular remains relatively constant. The morphological and topographical relationships between the opercular, the neurocranium, and the suspensory apparatus are also maintained during nandid evolution, indicating that the pronounced evolutionary changes in the feeding mechanisms have remained independent from the opercular bone. The size reduction of the subopercular is directly correlated with the elimination of the bone from the levator operculi-opercular apparatus-mandible coupling. The only function of the subopercular in *Polycentropsis* and *Monocirrhus* is to maintain the opercular suction pump during respiration.

e. The hyoid and branchial apparatus

The interactions between the branchial apparatus, neurocranium, and vertebral column have been discussed under "a." With the increase in depth of the suspensory apparatus in *Polycentropsis* and *Monocirrhus* comes an increase in the length of the interhyal (compare Figs. 24, 25 with 22). The interhyal increases the efficiency of the sternohyoid-hyoid-interopercular-mandible coupling. The longer interhyals may have evolved as a positional adjustment of the suspension of the hyoid apparatus to the greater depth of the suspensory apparatus. However, van Dobben (1937) has clearly demonstrated the functional role of long interhyals in the jaw mechanism. The increased height of the dorsal process of the urohyal in *Polycentropsis* and *Monocirrhus* is correlated with the increased efficiency of the pectoral girdle-pharyngocleithralis-lower pharyngeal-pharyngohyoideus-urohyal coupling, which protracts and retracts the fifth ceratobranchials, although it contributes to the positional adjustment in relation to the increased depth of the suspensory apparatus.

The suspension of the branchial apparatus from the neurocranium by means of the first pharyngobranchial does not vary among nandids, except for the increase in length of the first pharyngobranchial in *Polycentropsis* and *Monocirrhus*. The longer first pharyngobranchials may have evolved as a positional adjustment in response to the increase depth of the suspensory apparatus.

3. MUTUAL INFLUENCES BETWEEN RESPIRATORY AND FEEDING MECHANISMS

Many authors have stressed the intimate relationships between the feeding and respiratory mechanisms. Willem (1931), Woskoboinikoff (1932), Ballintijn and Hughes (1965), and Liem (1967b) have stated that feeding movements are basically respiratory movements at greater amplitudes.

Günther and Deckert (1960) have demonstrated elegantly the mutual influences between the feeding and respiratory mechanisms in *Harpodon nehereus,* which has a posteriorly displaced quadratomandibular joint.

In nandids there is a progressive reduction of the subopercular and branchiostegal apparatus in the series *Nandus, Afronandus, Polycentrus, Polycentropsis,* and *Monocirrhus.* However, the relative and absolute size of the opercular remains constant. The size reduction of the subopercular and branchiostegal apparatus will, therefore, result in a decrease in the contribution of the opercular suction pump to the total respiration. The progressive reduction of the role of the opercular suction pump is accompanied by a progressively more dominant buccopharyngeal pressure pump. Motion analysis has shown that in *Nandus* total respiration is performed by a balance between buccopharyngeal pressure pump and opercular suction pump. In *Monocirrhus* the opercular suction pump is virtually non-functional. The dominance of the pressure pump is realized by the larger volume of the buccopharyngeal pump, which is the result of the increase in depth of the buccopharyngeal pump. The larger the volume of the oro-pharynx, the larger the capacity of the pressure pump. The interopercular in *Polycentropsis* and *Monocirrhus* has become relatively independent from the respiratory functions, because of its mechanical involvements with the vertical reorientation of the levator operculi-opercular apparatus-mandible coupling. The size reduction of the subopercular is correlated with the strong selection pressure for an increased efficiency of the levator operculi-opercular apparatus-mandible coupling, which is accomplished by a vertical alignment of the coupling and the elimination of the subopercular from the coupling. The primary evolutionary trend is toward an increased efficiency of the predatory apparatus. The elimination of the subopercular by size reduction from the vertically reoriented levator operculi-opercular apparatus-mandible coupling enhances the speed and the degree of jaw opening and protrusion, both of which are essential adaptations for capturing large and elusive prey. It has been demonstrated from a functional anatomical standpoint that there is strong selection pressure for the evolving mechanisms underlying the exceptional speed and degree of mouth opening and protrusion. The progressive trend associated with the feeding mechanism and affecting the opercular apparatus, i.e., gradual rotation of the interopercular from a horizontal to a vertical position, is a primary evolutionary trend under strong selection pressure. The size reduction of the subopercular and the progressively diminishing role of the opercular suction pump of the respiratory apparatus in the series *Nandus-Afro-*

nandus - *Polycentrus* - *Polycentropsis* - *Monocirrhus* occur as a simultaneous, but secondary evolutionary trend. The secondary trend evolves as a mechanical co-adaptation to the primary trend and culminates in the loss of the original function of the opercular apparatus. The diminished role of the opercular suction pump is compensated for by the increased capacity of the buccopharyngeal pressure pump in *Polycentropsis* and *Monocirrhus*.

The diminished role of the opercular suction pump has a great adaptive ethological meaning. The stealthy approach of the nandid predator toward its prey is made by drifting slowly and imperceptibly with the head at a downward angle, exposing the cream-colored interorbital line in the split head pattern (Barlow, 1967a). Lateral movements of the opercular apparatus would certainly be obvious and alert the prey. The movements of the buccopharyngeal pressure pump, on the other hand, are invisible to the prey during the predator's approach with the head at a downward angle.

The movements of the mechanical units of the head during feeding are exceedingly different from those during respiration in nandids. However, the pattern of neurological control of deglutition and the respiratory cycle seem closely interrelated. Protraction of the upper and lower pharyngeal bones during deglutition coincides with the inspiratory phase of respiration, whereas retraction of the supra- and infrapharyngeal bones always occurs during the expiratory phase.

4. THE PHYLOGENY OF THE NANDIDAE

Regan (1913) has placed the Nandidae in the suborder Percoidei. Most authors (Jordan, 1923; Berg, 1940; Bertin and Arambourg, 1958; Freihofer, 1963; Greenwood et al., 1966; Monod, 1968) have followed Regan's classification. Recently Gosline (1968, pp. 3, 10, 12) has suggested that the Nandidae have phylogenetic affinities with the Anabantoidei. The alleged resemblances between the anabantoids and nandids are summarized as follows: (1) the presence of an expanded auditory (saccular) bulla on the cranium; (2) the two groups have the same, rather primitive, percoid caudal skeletons; (3) the nandids, like the anabantoids, are freshwater fishes with a distribution center in southeast Asia; (4) the presence of teeth on the parasphenoid.

Let us examine these four characters in greater detail.

The presence of an expanded saccular bulla is restricted to one nandid genus only, i.e., *Nandus* (Fig. 4). All other nandids lack expanded saccular bullae (Figs. 5–8). The exceptionally large saccular bullae in anabantoids is functionally related to the extraordinary hearing abilities realized by the utilization of the air in the suprapharyngeal cavity as a resonating chamber (Schneider, 1941; Liem, 1963, 1967a). The presence and absence of enlarged saccular bullae seem to vary considerably in acanthopterygians (e.g., Patterson, 1964) and it seems scientifically unwarranted to use this character as a phylogenetic indicator of any weight without a thorough understanding of the nature of the interactions between this variable structure and the governing selection forces.

The caudal skeleton of the nandids does resemble that of some anabantoid representatives (Monod, 1968; Patterson, 1968). However, the caudal skeleton of *Afronandus* differs significantly from that of the Anabantoidei (Fig. 27).

The center of distribution of the Nandidae is not southeastern Asia (Darlington, 1957). Only one genus (*Nandus*) occurs in southeast Asia. Two genera (*Afronandus, Polycentropsis*) are found in West Africa, while *Polycentrus* and *Monocirrhus* represent the South American genera. Gosline (1968) is, therefore, in error by using this character as evidence in establishing phylogenetic relationships between nandids and anabantoids.

The presence of teeth on the parasphenoid in nandids is restricted to *Nandus*. All other nandids lack parasphenoid dentition. However, Gosline (1968) has used the presence of parasphenoid teeth as one of the indicators of phylogenetic relationships between Anabantoidei, *Ophicephalus, Luciocephalus,* and nandids, although he has noted ". . . a postulate of reappearance [of the parasphenoid teeth] is preferable to one of inheritance." However, reappearance of lost structures has a genetic basis. DeBeer (1958) has demonstrated that lost structures may reappear during evolution by reconstitution of the *original* genetic conditions by suitable recombination of genes. The distinction between "reappearance" and "inheritance" is purely speculative. Gosline ignores the fact that the uniqueness of the Anabantoidei lies in the presence of prominent pharyngeal processes of the parasphenoid and basioccipital (Liem, 1963), unparalleled by any perciform, and perhaps, by any other acanthopterygian. Since the majority of the nandids lack parasphenoid teeth, the alleged resemblance in respect to this character between the anabantoids and nandids should be rejected.

The only valid resemblance between nandids and some anabantoids is, therefore, restricted to the caudal skeleton, with the important exception of *Afronandus.*

The Nandidae share all percoid characters listed by Regan (1913) and should be regarded as a highly predaceous family of the suborder Percoidei. Jordan's (1923) suggestion that *Polycentrus, Polycentropsis,* and *Monocirrhus* form a separate family, Polycentridae, as contrasted to the Nandidae (*Nandus, Pristolepis, Badis*) has no morphological basis. *Nandus* differs from Jordan's Polycentridae in the following features: the broad nasals; teeth on ectopterygoid, third hypobranchials, palatine, prevomer, and parasphenoid; the double articulation of the joint between palatine and neurocranium; three heads in the adductor mandibulae muscles; the absence of the craniopalatine ligaments; presence of a primordial ligament in the jaw apparatus. With the discovery of *Afronandus* by Meinken (1954, 1955) the gap between *Nandus* and Jordan's Polycentridae has been narrowed significantly. The differences between *Nandus* and Jordan's Polycentridae can be reduced to one character complex specifically adaptive to swallowing progressively larger prey. In the series *Nandus - Afronandus - Polycentrus - Polycentropsis - Monocirrhus* we find changes leading toward a highly specialized adaptive pattern for swallowing large prey *in toto.* Because of the intricate mutual influences within and between mechanical units, the morphological changes do not evolve singly. As discussed in the three previous subchapters, co-adaptation of mechanical units leads to the development of character complexes. The differences between the two morphological extremes among nandids, i.e., *Nandus* and *Monocirrhus,* can be reduced to one character complex reflecting an adaptation to swallowing large prey *in toto* in *Monocirrhus.* Intermediate stages are represented by *Polycentrus* and *Polycentropsis.* The co-adaptive progressive evolutionary trends in the series *Nandus-Afronandus-Polycentrus-Polycentropsis-Monocirrhus* are: reduction of teeth on relatively non-mobile bones; lengthening of the jaws; reorientation of levator operculi-opercular apparatus-mandible coupling from a horizontal to a vertical position; incorporation of the palatine into the jaw apparatus; and reduction of the opercular suction pump. The functional interdependency of the evolutionary trends has been discussed in the previous subchapters. The morphological changes are so gradual and functionally interdependent that we have to consider the five genera closely related. The subdivision into two families or subfamilies has no evolutionary morphological basis. The five genera are, therefore, classified into one family, the Nandidae.

Nandus and *Afronandus* seem to represent the most generalized or ancestral nandids, since they have the most generalized feeding apparatus. Contrary to Meinken's (1954) original description, no teeth have been found in the type specimen of *Afronandus* (British Museum, BM 35.355) on the prevomer, parasphenoid, palatine, and ectopterygoid. The loss of the palatal teeth may represent a derived character, but the absence of a complete, secondary neural arch on the second pre-ural vertebra represents an ancestral condition.

Polycentrus occupies an intermediate position in the evolutionary trend leading from *Nandus* to *Monocirrhus*.

Polycentropsis and *Monocirrhus* can be regarded as evolutionary advanced stages.

It is not implied that the evolutionary series *Nandus-Afronandus-Polycentrus-Polycentropsis-Monocirrhus* represents a single phylogenetic line. However, it reflects the best documented evolutionary pathway. *Nandus* and *Afronandus* are at the beginning of the trend and may exhibit a greater resemblance to the ancestral phylogenetic nandid stock than do the other living nandids.

The genus *Badis*, previously classified with the Pristolepidae by Regan (1913), has been reclassified (Barlow et al., 1968) in a new family Badidae with anabantoid affinities. *Pristolepis* has no phylogenetic relationships with the Nandidae (Liem, in preparation).

In the absence of detailed functional anatomical data on other percoid families, the phylogenetic position of the Nandidae within the suborder Percoidei is difficult to postulate. However, we may conclude that the most generalized nandids have reached a more "advanced" evolutionary stage than many other percoids (e.g., *Lates*, *Epinephelus*, many Percidae, Monodactylidae). So far there is no evidence for the direct phylogenetic derivation of the Nandidae from the Beryciformes.

The historical factors underlying the geographical distribution of living nandids remains unknown since no data are available on the possible dispersal routes. No new, well-documented theories can be added to those of Myers (1938) and Darlington (1957).

5. RETROSPECT

Functional anatomical analysis has been instrumental in explaining the evolutionary mechanisms underlying the morphological differences of the nandids. The functional approach has furnished answers to why and how the adaptive patterns of the Nandidae have evolved. Most of the differences are correlated with differences in the relative growth of bones in certain mechanical units and couplings, and in the degree of ossification of certain cartilages and connective tissue membranes. However, the functional and morphological consequences of these relatively minor ontogenetic differences are deceptively far-reaching and can be detected and evaluated only by functional anatomy. It is conceivable that relatively minor genetic differences govern the changes in relative growth of bones and ossification centers. But, the changes induced by these minor genetic differences give rise to a chain reaction of functionally-coadaptive changes in neighboring regions within mechanical units or in remote areas belonging to an associated coupling. The functional method has revealed the nature of the coadaptive interdependency of seemingly large numbers of morphological differences between nandids. The morphological diversity in nandids has been reduced to one functionally-coadaptive and mutually-interdependent character complex, which has evolved by relatively minor genetic changes. The close phylogenetic relationships between the nandids have, therefore, been demonstrated by a comparative functional anatomical approach.

Summary

The percoid family Nandidae, comprising *Nandus, Afronandus, Polycentrus, Polycentropsis,* and *Monocirrhus,* is characterized as follows: Neurocranium with a rostral fossa involving frontals and ethmoid, and reaching posteriorly to the supraoccipital. Two parietal crests on epiotics, parietals, and posterior halves of frontals. Median supraoccipital crest on supraoccipital. No subocular shelf. Hyomandibular with a rounded anterior head, and an elongate, straight posterior head. Anterior margin of the body of the hyomandibular is produced into a dorsal spine of the metapterygoid. Large metapterygoid joined to symplectic process of hyomandibular. Vertical preopercular has a very short horizontal limb. Triangular opercular is directly connected to interopercular by interoperculo-opercular ligament. Jaws very long. Mandible at least three-fourths the length of the neurocranium. Premaxillae without articular processes. Twenty-three vertebrae of which the precaudals have parapophyses from the seventh or eighth.

Motion analysis and experimental procedures involving the surgical removal of various ligaments and bones have proved that jaw protrusion is caused by depression of the mandible in *Monocirrhus.*

Depression of the mandible is caused by three couplings: (1) The levator operculi-opercular apparatus-mandible coupling; (2) The sternohyoid-hyoid-interopercular-mandible coupling; (3) The suspensory abductors-suspensory apparatus-mandible coupling. All three couplings have to function to protrude the jaws fully.

The medial and anterior maxillomandibular ligaments transmit the downward force of the mandible to the upper jaws causing them to protrude.

The sternohyoideus muscle plays no role in abducting the suspensory apparatus.

Deglutition of large prey *in toto* proceeds in three phases: the gnathous, gnathopharyngeal, and pharyngeal.

During the gnathous phase the jaws are protracted and retracted alternately. Retraction of the jaws occurs while the suspensoria are greatly abducted. Retraction is caused by the adductor mandibulae muscles, while protraction proceeds through the action of the sternohyoid-hyoid-interopercular-mandible coupling, which is highly efficient because of the long interhyals.

During the gnathopharyngeal phase of deglutition, the pharyngeal apparatus is solely responsible for deglutition with the jaws performing only a secondary holding role.

The pharyngeal mechanism depends on protractory and retractory movements of the toothed upper and lower pharyngeal bones. Retraction of the upper pharyngeals is accompanied by adduction, resulting in a continuous grip on the prey by the teeth and is caused by contraction of the retractor ossium pharyngealium muscles. Protraction of the upper pharyngeals is accompanied by abduction, resulting in disengagement of the teeth from the prey and is caused by contraction of the levator arcuum branchialium externi muscles.

Protraction of the toothed lower pharyngeals is caused by the pharyngohyoideus and is accompanied by abduction through action of the pharyngocleithralis externus muscle. Retraction of the lower pharyngeal is caused by contraction of the pharyngocleithralis internus muscle and is accompanied by adduction through action of the transversus ventralis muscle.

Retraction of both upper and lower pharyngeals occurs simultaneously.

Protraction coincides with the inspiratory phase of the respiratory cycle, while retraction occurs during the expiratory phase.

In the series *Nandus-Afronandus-Polycentrus-Polycentropsis-Monocirrhus* we can recognize the following simultaneous, coadaptive, evolutionary trends which represent the development of adaptive mechanisms to swallowing large prey *in toto*: Increase in depth of the suspensory apparatus by the accelerated vertical growth of the preopercular and the rotation of the long axis of the quadrate from a horizontal to a vertical position. Increased height of the ascending process (coronoid process), which reduces the slack in the maxillo-mandibular ligaments by decreasing the bridge between upper jaw and mandible. Progressive mechanical dissociation of the palatine from the suspensory apparatus by the development of a flexible joint between pterygoid plate and palatine, which makes retraction of the premaxillae with abducted suspensoria possible. Reduction of tooth-bearing elements, which are limited to those bones that undergo protraction, retraction, abduction, and adduction. Alignment of the levator operculi-opercular apparatus-mandible coupling into a vertical position, which falls in the same line as the resultant force of the levator operculi muscle. Progressive reduction of the subopercular and branchial apparatus resulting in the loss of the opercular suction pump.

Size reduction of the subopercular is correlated with the selection pressure for an increased efficiency of the levator operculi-opercular apparatus-mandible coupling.

The increased efficiency of the predatory apparatus is a primary evolutionary trend, while the diminished role of the opercular suction pump represents a secondary evolutionary trend.

Nandidae have no phylogenetic affinities with the Anabantoidei. The nandids resemble relatively advanced Percoidei. *Nandus* and *Afronandus* seem to represent the most generalized nandids.

It is not implied that the evolutionary series *Nandus-Afronandus-Polycentrus-Polycentropsis-Monocirrhus* represents a single phylogenetic line. However, it reflects the best documented evolutionary pathway.

Most of the differences are correlated with differences in the relative growth of bones within mechanical units and degrees of ossification. Morphological consequences of these minor ontogenetic differences are deceptively far-reaching. It is suggested that relatively minor genetic differences govern the ontogenetic mechanisms that lead to a chain reaction of functionally coadaptive changes in neighboring regions within mechanical units or in remote areas belonging to an associated coupling.

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Addendum

While this publication was in press, an important reference: J. W. M. Osse, "Functional Morphology of the Head of the Perch (*Perca fluviatilis* L.): An Electromyographic Study," appeared in the *Netherlands Journal of Zoology,* **19,** pages 289–392 (1969).

Perca may be regarded as a rather generalized percoid and Osse's elegant and accurate functional-anatomical analysis of its feeding mechanism represents an excellent basis for future comparative anatomical studies of the head of other percoids and percoid derivatives. However, comparison should be made carefully. The techniques employed by Osse are unquestionably the most accurate and sophisticated ever recorded in the literature on teleost functional anatomy. Differences caused by differences in observational and recording techniques employed by subsequent authors working on other percoids and percoid derivatives should be carefully evaluated.

I will try to evaluate some of the interesting differences between *Perca* and the nandids. Generally, *Nandus* and *Afronandus* resemble *Perca* more closely than do the other nandid genera. Comparison is restricted to the respiratory and feeding mechanisms.

Respiratory mechanism

Osse has demonstrated conclusively that the sternohyoid-hyoid-interopercular-mandible coupling is not active during respiration in *Perca.* The postero-ventral movement of the urohyal recorded during quiet respiration is the secondary result of abduction of the suspensory apparatus by contraction of the levator arcus palatini muscle (see Osse, pp. 335, 337). It is very likely that *Nandus* and *Afronandus* have retained the opercular suction pump and that their breathing resembles that of *Perca.* The rotation of the opercular was probably too restricted to be recorded by ciné film. However, in *Monocirrhus* and *Polycentropsis* the opercular and branchiostegal apparatus are greatly reduced. In *Monocirrhus* respiration depends on the sternohyoid-hyoid-interopercular-mandible coupling. Abduction of the suspensorium is too limited to cause the excursions of the hyoid. During the evolution of the nandids there seems to have been a shift in the respiratory mechanism from a *Perca*-like type (*Nandus*), with complete reliance on the levator arcus palatini muscle, to the condition in *Monocirrhus*, with emphasis on the sternohyoideus muscle.

Feeding mechanism

One feature in the feeding pattern common to both *Perca* and all nandids is that during feeding, the levator operculi-opercular apparatus-mandible coupling initiates mouth opening and protrusion, but the final stages of mandibular depression and jaw protrusion depend on the sternohyoid-hyoid-interopercular-mandible coupling.

Osse (p. 367) has demonstrated the functional significance of the ratio of the distance between the quadratomandibular joint and anterior tip of the mandible and the distance between quadratomandibular joint and insertion site of the interoperculomandibular ligament. This ratio increases in the series *Nandus–Afronandus–Polycentrus–Polycentropsis–Monocirrhus* indicating a progressive increase in the efficiency of the couplings activated by the levator arcus palatini and sternohyoideus muscles.

The data on the functions of the sternohyoideus muscle during suspensorial abduction in nandids support Osse's findings (p. 364) that the levator arcus palatini is first to contract causing suspensorial abduction which is then followed by contraction of the sternohyoideus muscle. The role of the sternohyoideus muscle in abducting the suspensory apparatus is nil or, at the most, negligible.

In nandids suspensorial abduction causes mandibular depression. Osse (pp. 338, 343) found that in *Perca* strong contraction of the levator arcus palatini causes suspensorial abduction which pulls the hyoid apparatus postero-ventrally causing the mandible to drop via the ligament between hyoid and interopercular. In nandids, however, suspensorial abduction alone can depress the mandible partially, while the hyoid is stationary because of surgical removal of the connections between the hyoid, the interopercular, and suspensory apparatus. Extreme suspensorial abduction in nandids seems, therefore, to cause mandibular depression directly without the intermediary of the hyoid apparatus.

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